LONGITUDINAL DISTRIBUTION PATTERNS AND HABITAT ASSOCIATIONS OF JUVENILE COHO SALMON *ONCORHYNCHUS KISUTCH* IN TRIBUTARIES OF THE LITTLE SUSITNA RIVER, ALASKA

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A

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Abstract

Understanding how headwater streams function as rearing habitats for juvenile coho salmon *Oncorhynchus kisutch* is essential for effective population management and conservation. To inform habitat restoration activities within the Matanuska-Susitna Valley, Alaska, I determined upstream distribution limits, validated abundance estimates, and established fish habitat relationships in two headwater stream tributaries of the Little Susitna River in 2010-11. Using a low-effort, spatially continuous sampling approach and linear mixed-effects models, I related local- and landscape-scale habitat associations to abundance estimates. All-aged coho salmon composed approximately 98% of all fish sampled and inhabited the entire stream length to their upstream limits. Age-1+ fish resided in 64% and 44% of the stream length for the two sampled streams. The mean upstream elevation limit for all-aged fish in these streams was 278m and 267m. For age-1+ fish, the upstream elevation limit in the two streams was 275m and 238m. Percent slope at the distribution limit of all-aged fish was consistent across streams at 5%, whereas percent slope for age-1+ fish correspond to 4% and 6%. Elevation and percent slope consistently described upstream distribution limits among age classes. Therefore, we must consider these landscape features when prioritizing restoration projects in headwater streams.

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Chapter 1: Introduction

Ecological phenomena unfold across a wide array of spatial and temporal scales, necessitating an approach to hierarchically classifying stream system habitats for understanding physical and biotic processes driving demographics and distribution of salmon. However, viewing riverine environments in a continuous, rather than a discrete, hierarchical manner, provides further insight to the spatial heterogeneity of the stream-habitat mosaic and fish-habitat relationships occurring therein. This is critical for the conservation and management of juvenile coho salmon that use a complement of habitats over their life history. Because most studies on juvenile coho salmon ecology take place in low-gradient streams and side-channels, which often represent core habitats where these juveniles are most abundant, rather than the full range of available rearing habitat, including occupied areas of low abundance (peripheral habitats), a dearth of information exists regarding juvenile Pacific salmon in higher gradient headwater streams, also used by rearing juvenile salmon. Use of peripheral habitats like headwater streams represents a component of juvenile ecology that may contribute to long-term resilience of coho populations within the region by contributing to a wider range of life histories occurring in juveniles in the overall population (e.g., size at age, age and size at outmigration, etc.). The Little Susitna River, Alaska, is a model system to apply ecological theory in a management context. Relatively intact, it provides habitat for multiple Pacific salmon *Oncorhynchus spp.* runs. However, because this area is currently undergoing increased development, urbanization, and fishing pressure, Little Susitna salmon stocks are of conservation concern, particularly in headwater regions where much of this increased

development is proposed. This thesis examines juvenile coho salmon distributions and provides direction for future research within headwater streams of the Little Susitna River. This will allow for a more strategic and informed management of these populations with implications towards conservation and restoration practices occurring in the Matanuska-Susitna region.

This chapter is intended as an in-depth review of the literature relevant to the thesis study objectives, design, analytical approach, and interpretation of results. For this purpose, I review landscape ecology theory of riverine systems in the context of my research on juvenile coho salmon within headwater stream habitats. First, I briefly review concepts of landscape complementation and supplementation, then stream hierarchical theory. I follow this with a discussion of how spatial and temporal scales shape our understanding of ecological processes and set the stage for determining the most appropriate scale to investigate management questions of fish distribution and abundance, as are the purposes of this study. Based on this review, I argue that a continuous view of the habitat in either space or time provides additional insight that would be otherwise lacking in a more piecemeal or reach-specific study, where the reach is a sample unit on a linear spatial scale of 10 – 1,000 m, set between two points defined by arbitrary criteria (Frissell et al. 1986). Second, from a population perspective, I relate landscape theory to demographic processes of fish species within lotic environments. I examine how a continuous view of the landscape across spatial scales helps elucidate processes that drive distribution and abundance of juvenile coho salmon. Next, I focus

on the diversity of habitats required by juvenile coho salmon to complete their freshwater stage. Finally, I conclude by integrating these theories into formulating objectives of a case study that examines juvenile coho salmon distribution and provides direction for future research within headwater streams of the Little Susitna River, Alaska.

1.1 Landscape ecology in stream systems

The advent of landscape ecology (Forman and Godron 1986) brought about a paradigm shift in our understanding of fish habitat dynamics. Themes at the core of landscape ecology include understanding the relative spatial arrangement and relationships among distinct habitat patches, how patches vary within and across spatial scales, and the ability of patches to exchange materials and energy (Pringle et al. 1988; Wiens 2002). Fisheries managers have since recognized that the themes central to landscape ecology apply to the conservation of stream fishes and have helped establish links between spatially and temporally scale-dependent processes (Fausch et al. 2002). Landscape complementation and supplementation are important processes that provide insight for conservation and management of a species that require discrete habitats for completion of its life history (Tilman 1982; Frissell et al. 1986; Dunning et al. 1992). The presence of resources associated with summer rearing habitat patches, complemented by the close proximity of favorable overwintering patches with sufficient liquid water available, enables a region to support populations (Weins 1989; 2002). If any of these complementary habitats become unavailable, peripheral areas, such as headwater streams, can serve a supplemental role by providing alternative areas for rearing, overwintering, or

refugia, leading to greater resilience of populations to catastrophic or temporary disturbance (Weins 1989; 2002). If we neglect to sample and account for these peripheral habitats, or sample them sporadically in space and time, their functional importance to juvenile coho salmon may be underestimated.

1.2 Hierarchies in aquatic systems

Frissell et al. (1986) proposed a hierarchical structure for classifying the spatial extent of lotic habitat subsystems (e.g., segment between two major tributary junctions, reach) and temporal scales over which relevant developmental processes are most likely to occur. Their hierarchical organizational system is appropriate to second- or third-order headwater streams and limited in its organizational structure of the lateral dimension of floodplains and riparian areas. However, their framework provided a systematic approach for analyzing spatial and temporal patterns of physical and corresponding biological variation among headwater streams. Consequently, stream heterogeneity can now be classified across a variety of spatial scales from habitat unit systems (i.e., "pool/riffle") to watershed with temporal scales ranging from seasonally and annually to geological time scales (Frissell et al. 1986). Although operating within a hierarchical framework provides an understanding of the spatial arrangement of habitats comprising the stream mosaic, viewed in a biological context, it is the unique habitat requirements and migratory movements of aquatic species that dictate appropriate spatiotemporal scales for investigation (Schlosser and Angermeier 1995).

Recognition that ecological phenomena unfold across a wide array of scales led to the development of nested hierarchical models (Allen and Starr 1982). Central to hierarchical theory is how interactions at one level may or may not influence interactions at another (Frissell et al. 1986; Urban et al. 1987). For example, hillslope and channel processes greatly affect stream channel geomorphology by contributing large woody debris and sediments into streams (Montgomery 1999). However, attempting to predict stream channel geomorphology at a higher hierarchical level (e.g. watershed or basin) may not reveal these patterns. Similarly, pool and riffle morphology sequences along the length of a stream are determined, in part, by the slope of the landscape over which it flows. The slope, in turn, is affected by hillslope processes, sediment inputs, and flows, which are controlled by watershed area and topography.

Scheurer et al. (2003) exemplified the effects of nested hierarchies while investigating mechanisms influencing the persistence of the brassy minnow *Hybognathus hankinsoni* at three hierarchical levels (basin, segment, and habitat unit). They determined recruitment at a critical life stage was driven by landscape level drying processes, suggesting the importance of large-scale processes that create and maintain temporary habitats (e.g. inundated vegetated floodplains), rather than processes occurring at a local level. The authors noted that understanding the process of recruitment in this system would not be apparent at solely the local scale. In fact, only by exploring multiple levels of the hierarchy were they able to determine mechanisms driving persistence. These conclusions support the ideas proposed by Forman and Godron (1981; 1986) that

no single scale is appropriate for investigating all ecological problems, and special attention directed to the appropriate scale at which the process occurs is essential (Frissell et al. 1986; Wiens 1989; Fausch et al. 2002; Wiens 2002). However, it is important to note that some landscape metrics are scale dependent (e.g., stream sinuosity and slope are scale dependent based upon the length of stream reach used). Therefore, a hierarchical view of space and time is crucial for understanding the ecological processes operating in stream systems (Frissell et al. 1986; Schlosser 1991; Fausch et al. 2002; Wiens 2002; Benda et al., 2004).

Developing a hierarchical approach emphasizing the importance of scale and understanding how it relates to demographic processes of fish species is critical in the management and conservation of fish species (Urban et al. 1987; Weins et al. 1993). However, studies of aquatic habitat and fish-habitat relationships within riverine systems have most often occurred at the reach scale (Frissell et al. 1986; Imhof et al. 1996) - primarily due to this being the most common spatial scale used by managers investigating distribution patterns of fish. By investigating beyond the reach scale, managers can view the landscape in a continuous manner (i.e., spatially continuous sampling along an entire stream network or stream segment in the stream hierarchy, hereafter continuous sampling), and establish spatial relationships between the patchy habitat landscape mosaic and the abundance of organisms occurring therein (Fausch et al. 2002).

1.3 Continuous sampling in a landscape context

Studies that relate physical habitat structure and anadromous salmonids are common (Nickelson et al. 1992), but little has been done to investigate these relationships using continuous sampling designs. Many juvenile coho salmon studies focus on demographic properties (e.g., abundance) of fish populations and physical relationships between habitats. Often the study area consists of a few representative reaches, 10 – 200 m in length, located within one or more stream segments. Physical conditions most often recorded in these studies include channel dimensions, substrate composition, cover and refuge, streambank and shoreline condition, and riparian vegetation (Hankin and Reeves 1988; Torgersen et al. 2006). However, salmonids often use a complement of these habitats over larger spatial extents throughout their life history (Figure 1.1).

An attempt to understand the processes that drive distribution and abundance of organisms within the aquatic environment involves simple questions met with difficult answers. Researchers and managers often attempt to address these questions on a single spatial or temporal scale and lose critical information on causal relationships between habitat and fish populations. Processes, whose patterns emerge on one level, may disappear or become less obvious on another organizational level (Frissell 1986; Schlosser 1991; Schlosser and Angermeier 1995; Fausch et. al., 2002). Therefore, sampling over multiple spatial scales and in a continuous manner may help elucidate mechanisms driving demographics and distribution. By incorporating continuous habitat and abundance sampling of cutthroat trout (*Oncorhynchus clarkii clarkii*) on multiple

spatial scales, Gresswell et al. (2006) developed a hypothesis regarding the physical processes and structures influencing abundances at the catchment level across western Oregon. Torgersen et al. (2006) investigated distribution and aquatic habitat associations of fish assemblages within spatially continuous stream segments. Sampling in a continuous manner, and over large spatial scales, allowed them to examine both whole-stream patterns and investigate stream segments at finer spatial scales (e.g. reach length), providing multiple spatial resolutions for detecting patterns in fish-habitat relationships. Given that rare or unique features within stream networks can be disproportionately important to stream fishes, the need for increased use of continuous sampling in space and time is essential so these habitats are not overlooked (Fausch et al. 2002). Research incorporating random or stratified random sampling patterns often misses these areas within a stream, therefore failing to capture an accurate picture of the fish population sampled (Hankin and Reeves 1988; Williams et al. 2011).

Continuous sampling of thermal environments within the stream network may also provide insight into causal factors constraining the distribution and abundance of fishes within a stream over time. Investigating thermal patchiness in streams as refugia for Chinook salmon (*Oncorhynchus tshawytscha*), Torgersen et al. (1999) sampled stream temperature in a continuous manner within upper basins of the John Day River, Oregon. Sampling at multiple spatial scales revealed a non-uniform distribution of Chinook salmon at the reach scale. In marginal habitats for species on the fringe of

environmental tolerances, the ability to identify suitable habitats is critical for the conservation and management of a species.

1.4 Ecology of juvenile coho salmon

As with the heterogeneity of physical habitats, localized heterogeneity in stream temperatures contribute to conditions favorable for juvenile coho salmon to complete their life history. This is particularly the case within snowmelt and glacially driven systems, where headwater areas provide cool water refugia over mainstem areas during summer baseline flows and thermal maximums (Meyer et al. 2007). In addition to summer high temperatures, it is equally important to understand if winter water temperatures are sufficient as refugia from freezing conditions and capable of supporting overwintering populations. Understanding the range of thermal conditions that exist throughout habitats accessible to juvenile coho salmon will provide insight into whether or not these areas fall within the thermal niche of the species and shape our understanding of factors that limit or restrain juvenile coho salmon distribution within headwater streams.

A large amount of research on nursery and rearing habitats suggests juvenile coho salmon are found in greatest abundances in slow-velocity habitat areas, including backwaters, floodplains, oxbow lakes, upland sloughs, beaver ponds, and a variety of off-channel habitats (Bisson et al. 1982; Bryant 1983; Murphy et al. 1989; Bjornn and Reiser 1991; Collins et al 2003; Pollock et al. 2004; Quinn 2005) hereafter referred to as ‘core’

rearing habitats. Areas of low water velocity allow fish to optimize their energy budgets by allocating greater amounts of energy towards growth and development rather than maintaining a constant swimming position within the water column. This trade-off and allocation of energetic resources allows them to attain a larger body size during their early life stages, improving survival (Werner and Gilliam 1984; Quinn and Peterson 1996). Additionally, the high surface area to shoreline ratio associated with slower velocity habitat morphologies results in a greater quantity of shallow-watered habitat areas. These areas often contain emergent vegetation that provides cover from predators. Further, shallow pond margins warm more quickly during summer periods than open water areas, enabling juvenile coho salmon to optimize physiological performance.

Although these slow-water habitats often form the core of habitat selection for juvenile coho salmon, they are by no means the only habitat type occupied during this crucial life stage. Juvenile coho salmon exhibit a high degree of plasticity in habitat selection. In case of overcrowding or mainstem habitat unavailability, peripheral habitat configurations adjacent to core areas of high abundance may play a critical complementary or supplemental role in providing nursing and rearing areas. The relative contribution of peripheral habitat space to salmon production is unknown. Upon emergence from the gravel, juvenile coho salmon will take up position and defend territories within suitable areas of the stream channel (Quinn 2005). During times of high abundance, fish unable to defend territories may move to alternate rearing habitats that provide supplemental habitats.

It has been proposed that estuarine environments provide such peripheral habitat in the case of freshwater habitat saturation during their first year of life (Hoem-Neher et al. 2013). After emergence from the gravel in April - June, a large number of fry may move downstream as "nomads", a term first used by Chapman (1962), giving rise to the concept of surplus fry. Koski (2009) proposed this behavior as a life-history strategy coho salmon use to take advantage of more productive diverse habitat opportunities located downstream in estuarine environments.

Fish experiencing density-dependent processes in side-channel habitats may also move upstream to find alternative or supplementary rearing habitat. Although coho salmon are frequently documented in headwater stream environments (Johnson and Weiss 2007), we are not aware of any work documenting the use of, or relative contribution of, high-gradient headwater streams as rearing areas for juvenile coho salmon. These peripheral, high gradient (e.g., >2% slope) streams provide habitat features consistent, if not optimal, with the needs of juvenile coho salmon for completion of different life stages and have potential for playing this role (Rosenfeld et al. 2000).

1.5 Early ecology of coho salmon

Coho salmon require a diversity of habitats over their freshwater stage (Northcote 1997). Egg deposition upon the substrate is a function of adult female site selection. Upon fertilization, the adult female will bury the embryos and, unless disturbed, they will

remain in place during embryonic development. Physical variables attributed to redd site selection include water velocity, depth, and substrate size. However, preferred habitat selection by adult females depends upon embryonic development needs, particularly oxygenated water flow within the hyporheic zone and suitable gravel size (Quinn 2005). Average gravel size selected for redd construction is a function of the length of adult female coho (Kondolf and Wolman 1993). Newly hatched eggs, or alevins, exhibit vertical and horizontal movements within the interstices of the substrate but rarely exceed an area of 200 cm^2 (Dill and Northcote 1970). Therefore, oxygenated water flow within the hyporheic zone and suitable gravel size appear critical over these life stages.

In addition to habitat requirements varying over life stage, they may also shift seasonally. For example, juvenile coho will occupy warm, food rich, habitats in summer and thermally stable habitats with liquid water available in winter (Quinn 2005). Upon emerging from the gravel in early spring, juvenile coho enter the water column as free-swimming individuals called fry and take up positions within areas of low water velocity, often along stream margins where they avoid predators and high flows (Ruggles 1966; Bisson et al. 1982), actively seeking to colonize areas in search of rearing habitat (Au 1972). Older age classes of coho salmon, also known as parr, returning to summer feeding and rearing areas may occupy these same regions and set up territories in deeper pools with greater habitat complexity (Rosenfeld et al. 2000). Juvenile coho salmon may rear in freshwater for up to three years prior to migrating to sea (Quinn 2005). Parr not returning to summer feeding habitats will undergo the parr-smolt transformation, which

for coho in Alaska, occurs from Mid-May until early July (Drucker 1972; Carlon 1992; Thedinga et al. 1994).

During the spring and early summer, growth is rapid and slows during late summer at low flow when food and space become limiting, thereby increasing competition. Higher flows associated with early fall freshets cue coho salmon movements into secondary channels, sloughs, backwatered areas, wetlands, and other off-channel habitats that were previously inaccessible during the regular season (Cederholm and Scarlett 1981). As water temperatures decline at the onset of fall, they seek structurally complex habitats that provide refugia from freezing water temperatures, ice processes, and predation (McMahon and Hartman 1989). Over-winter habitat in freshwater for juvenile coho salmon consists of areas of low stream velocities, deep watered areas with woody debris cover, side channels, off-channel pools, and beaver ponds (Murphy et al. 1989; Reynolds 1996). Movements during spring immigration, from over-winter areas to summer rearing and feeding areas, is a behavioral response to summer territorial redistribution (Cederholm and Scarlett 1981).

1.6 Study area

The Little Susitna watershed drains over 160 km² within the Cook Inlet region of southcentral Alaska and originates at the Mint Glacier on Montana Peak in the Talkeetna Mountains north of Palmer, Alaska (Figure 1.2). The river flows southwest for approximately 177 km, discharging into upper Cook Inlet approximately 21 km west of

Anchorage and 11 km east of the mouth of the Susitna River. Annual precipitation estimates within the region during 2010 and 2011 were 607 mm and 604 mm, respectively (Western Regional Climate Center weather station, 508976, Talkeetna, WSCMO AP, Alaska). Streamflow estimates during the 2010 and 2011 study period were approximately 154.5 and 163.1 f^3s^{-1}, respectively (USGS gauge station, 15290000, L Susitna R NR Palmer, AK). Riparian zones of headwater streams located in the upper basin are dominated by a mixed forest type of black cottonwood (*Populus balsamifera ssp. trichocarpa*), Sitka alder (*Alnus crispa spp. sinuate*) and white spruce (*Picea glauca*), with an understory of devil's club (*Oplopanax horridus*), cow parsnip (*Heracleum lanatum*), ladyfern (*Athyrium filix – femina*) and horsetail (*Equisetum spp.*). The study area is dominated by glaciofluvial deposits in the lower reaches occurring within the floodplain of the Little Susitna River, and bedrock and alluvial depositions in the upper reaches and extents within recharge areas. The Little Susitna River supports runs of Chinook salmon *O. tshawytscha*, coho salmon *O. kisutch*, sockeye salmon *O. nerka,* pink salmon *O. gorbuscha*, and chum salmon *O. keta* (Ivey et al. 2009). Small headwater streams within the upper Little Susitna drainage are high gradient (channel slope >2%), single order systems known to contain juvenile salmon (Johnson and Weiss 2007; Curran and Rice 2009; Davis and Davis 2009); however, the extent to which these headwater streams are used over this life stage is unknown.

The Little Susitna River coho salmon sport fish harvest is the second largest freshwater fishery for coho salmon in Alaska (Ivey et al. 2009). Typically, managers rely

on run enumeration and population modeling to manage fisheries of this kind; however, retention of key spawning and rearing habitats are critical components of any effective management plan. Understanding how these habitats function spatially and temporally across the landscape and how they respond to anthropogenic disturbances is vital for the long-term stewardship of productive and diverse salmonid populations within the Matanuska-Susitna Valley. The region is affected by ongoing development near the city of Anchorage and nearby towns of Wasilla and Palmer; however, it has potential as an example to other urban locations in the United States on how to continue human development while maintaining aquatic habitat integrity and environmental sustainability. Without a better understanding of the ecology of surrounding systems and the nature of human impacts, this goal is unattainable. In addition, managers require research to inform and prioritize ongoing restoration, preservation, and development activities.

The upper Little Susitna drainage is a relatively intact system with multiple Pacific salmon runs; however, increased development and urbanization in the area, an established and expanding road system, and increased recreational and commercial fishing pressure on salmon stocks are threats that require management consideration. Data on salmon stocks in the area are limited; we lack a full understanding of adult salmon spawning habitat distribution, juvenile rearing habitat, and what habitat factors limit the distribution and production of Pacific salmon. Restoration and conservation efforts are presently underway in the upper Little Susitna drainage; in particular, managers are replacing culverts to increase the stream length and habitats available to

juvenile salmon. However, it is difficult to assess the effectiveness of these restoration activities without a better understanding of the diversity and rearing potential of habitats upstream of culvert replacements. Prioritizing which culverts to replace is based solely on the length of habitat upstream of the culvert that would then be available to salmon. However, due to a lack of information and research, little consideration is given to the relative ability of these areas to support juvenile salmon populations, particularly older age classes (age 1 and over) that may be using them for rearing purposes. Our study is the first in the drainage to address upstream distribution limits of juvenile coho salmon and potential use of these headwater habitats. Differences among upstream headwater habitat availability and thermal characteristics between headwater streams could affect the use of these areas by juvenile salmon.

Finally, increased human development and urbanization around the cities of Anchorage and Wasilla have impacted stream biotic integrity and will do so in the upper Little Susitna region, where this research occurred. However, the extent and severity of impact will vary based on habitat quality; this information is needed to predict the impacts of ongoing and planned suburban expansion in the region. Given the variety and importance of management concerns in this region, information defining the habitat requirements and preferences of juvenile coho salmon is both important and timely. Prior work on coho salmon and related species has emphasized a variety of potential habitat features that may be important.

To address these management concerns, I conducted a two-year study within the Little Susitna River system of southcentral Alaska to examine what habitat conditions affect and limit the distribution of juvenile coho salmon in headwater streams of this watershed. My primary objective was to determine longitudinal distribution of all juvenile coho salmon and age 1+ size classes within this system and associate spatial patterns of juvenile fish distributions with habitat features, including thermal characteristics, gradient, and instream habitat. Research conducted in 2010 focused on assessing habitat conditions and identifying upper distributional limits of juvenile coho within headwater streams. Sampling of stream habitat units to investigate distribution patterns occurred during July, August, and September. Research conducted in 2011 focused on validating single-pass estimates of juvenile coho salmon relative abundance by cohort within headwater streams of the Little Susitna River drainage.

1.7 Research objectives

The overarching goal of this project was to determine juvenile coho salmon distributional limits, abundance, and habitat use in headwater streams of the Little Susitna River to inform ongoing restoration efforts in the region. Individual goals and objectives were as follows:

Goal 1: Validate the use of counts from single-pass electrofishing techniques as an alternative for fish abundance in headwater streams of the Little Susitna drainage.

Objective 1. Using closed-population mark-recapture techniques, measure the abundance of juvenile coho salmon in easily accessible 200 m reaches of headwater streams.

Objective 2. Measure habitat features of 200 m reaches that may affect sampling efficiency (e.g., pool depth, woody debris, undercut banks).

Objective 3. Develop logistic regression models of single-pass sampling efficiency based on habitat features. Correct CPUE data for each tributary using validation models to better reflect actual fish abundances and confidence in abundance estimates.

Goal 2: Determine and characterize the upstream limits of juvenile coho salmon by age and size class in headwater streams of the Little Susitna River.

Objective 1. Sample three headwater streams of the river in a continuous manner to the upstream extent of juvenile coho salmon distribution.

Objective 2. Use length-frequency analysis to determine the age of captured individuals and describe the distribution within the tributary systems by age class.

Goal 3: Characterize available habitat in headwater streams and relate the distribution and validated abundance patterns of juvenile coho salmon (all captured and age 1+ individuals) to these habitat characteristics.

Objective 1. Use a continuous, streamwide approach to collect habitat information at 200 m reach lengths. Further, take elevation measures to supplement and validate information gathered remotely.

Objective 2. Use regression techniques to develop models predicting the presence and absence of juvenile coho salmon by age class in stream reaches based on a subset of habitat variables collected. If coho are continuously present along the occupied stream reach, identify barriers to the upstream extent (i.e., distance from main stem river, gradient, elevation, or thermal properties of the site).

Objective 3. Model validated abundance estimates (number of fish captured per reach sampled) of juvenile coho salmon relative to habitat characteristics of the reach to identify important areas of high juvenile productivity and corresponding habitat features.

Goal 4: Determine short-term temporal changes in distribution of coho salmon juveniles in headwater streams between July and September.

Objective 1. Engage in repeat sampling of the upstream extent of juvenile coho for all study streams to determine changes in occupied reaches over the growing season.

To achieve these objectives, I sampled selected headwater streams in the Little Susitna drainage using a continuous, repeat sampling technique to determine spatial patterns in fish distributions (Bateman et al. 2005). The lower effort associated with this technique allows an increase in sampling extent to the watershed level (Bateman et al. 2005; Gresswell et al. 2006; Torgersen et al. 2006; Torgersen et al. 2007), but reduces the precision and accuracy of CPUE as a surrogate measure of abundance (Rosenberger and Dunham 2005). Therefore, my primary objectives focused on validation of a sampling efficiency model in conjunction with identifying the distributional patterns of coho salmon age classes, rather than relative abundance over the sampling area. I conducted a streamwide assessment of habitat. I included variables known to be important for juvenile salmon and sampling efficiency of salmonids, in particular, pool frequency, wood debris, stream size, gradient, elevation, and distance from mainstem river habitat.

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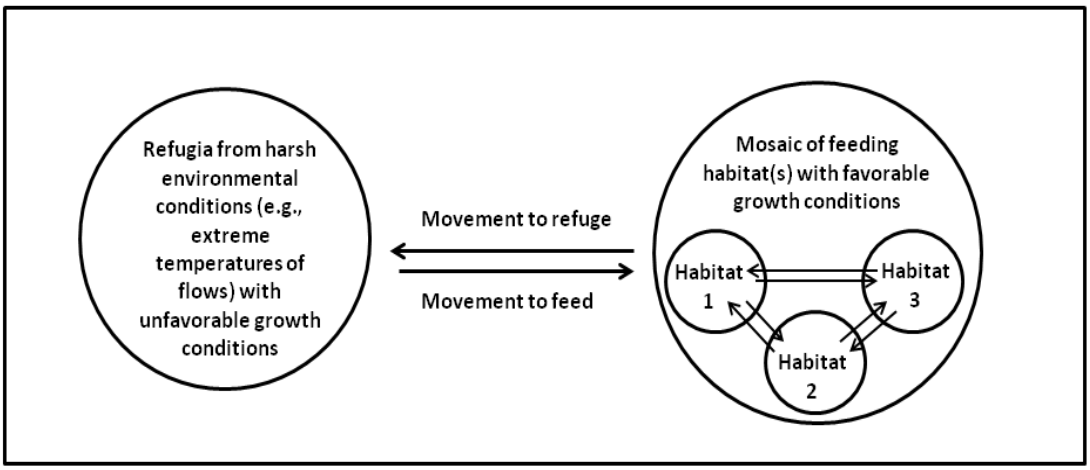

Figure 1.1 Schematic of a life cycle of stream fish. Schematic of a life cycle of stream fish with emphasis on juvenile coho salmon patterns of freshwater habitat use and movements (adapted from Schlosser and Angermeier 1995; based on Jones 1968; Northcote 1978; and Schlosser 1991).

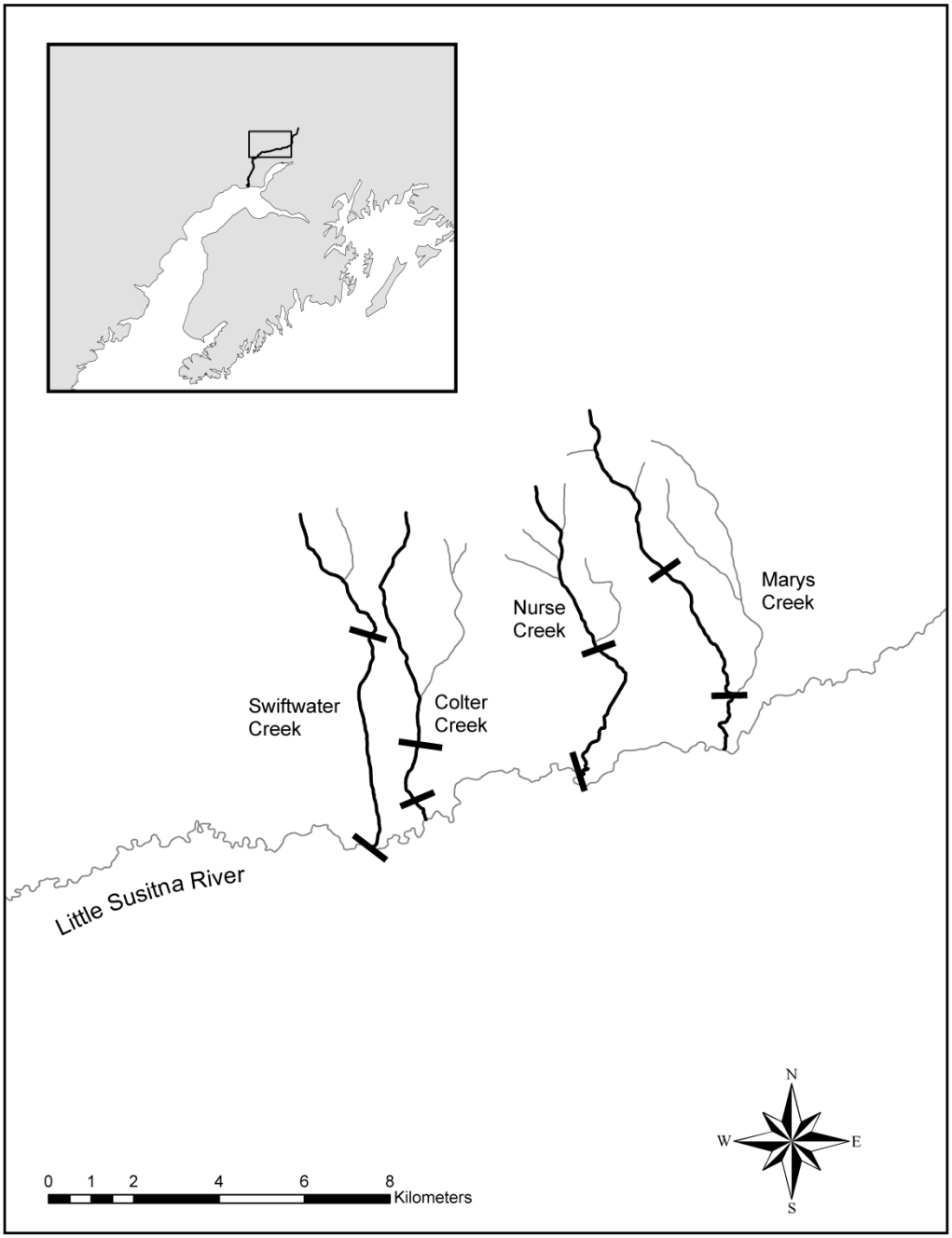

Figure 1.2 Study area map. Inset map of the Kenai Peninsula and upper Cook Inlet, Alaska. Study areas within Little Susitna tributaries shown between bold hash marks.

Chapter 2: Effectiveness of low-effort, single-pass backpack electrofisher use for estimation of juvenile coho salmon abundance in Alaskan headwater streams[1].

2.1 Abstract

Without fully understanding the effectiveness of capture methods, the use of techniques with low or inconsistent sampling efficiency could lead to erroneous estimates of abundance, particularly when sampling efficiency varies over a range of habitat types. Although an increase in sampling intensity can improve sampling efficiency and estimator precision, its cost can limit a study's spatial extent. A low-effort approach may be preferred for landscape scale studies of fish distribution and abundance; however, this requires information on whether the low-effort sampling is vulnerable to habitat-mediated bias and imprecision of the estimator. To determine how habitat features affected sampling efficiency of juvenile coho salmon *Oncorhynchus kisutch* in headwater streams of the Little Susitna drainage, Alaska, we validated low-effort backpack electrofishing methods with closed population mark-recapture sampling. We found that habitat characteristics, such as stream size and density of wood debris, had no measurable or consistent effect on sampling efficiency within the range of conditions present in these headwater systems, and single-pass catch explained 94.8% of the observed variation in

[1]Foley, K.M., A.E. Rosenberger, and F.J. Mueter. 2014. Effectiveness of low-effort, single-pass backpack electrofisher use for estimation of juvenile coho salmon abundance in Alaskan headwater streams. Prepared for submission in North American Journal of Fisheries Management.

log-transformed mark-recapture estimates. This suggests that low-effort methods in headwater streams of the Little Susitna River can approximate actual fish numbers without accounting for habitat covariates that may influence sampling efficiency, and the advantage of sampling a greater spatial extent may sufficiently offset any concerns over low estimator precision.

2.2 Introduction

Biologists and fisheries resource managers require reliable methods to assess the abundance of stream fishes. One method of capture commonly used to sample wadeable, cold-water stream fishes is the backpack electrofisher (Reynolds 1996; Dunham et al. 2009). However, backpack electrofisher sampling efficiency can be affected by physical habitat characteristics and species or individual characters of the target organism (Kruse et al. 1998; Peterson et al. 2004; Rosenberger and Dunham 2005). Environmental characteristics affecting electrofisher sampling efficiency include: water conductivity, substrate type (Peterson et al. 2004), instream cover (Thompson and Rahel 1998; Kruse et al. 1998), surface area, and stream size (Rosenberger and Dunham 2005). These characteristics either contribute to habitat complexity or reduce the effectiveness of electrical fields in the water (Reynolds 1996). For a study relying on reliable estimates of fish abundance, validation of electrofishing methods over the range of anticipated conditions is crucial.

High-effort approaches for sampling fish (e.g., 4-pass electrofishing, mark recapture estimates) generally involve higher sampling efficiency and decreased, or more predictable, bias when compared to low-effort approaches (Rosenberger and Dunham 2005). However, these methods are costly and time-intensive, limiting the spatial extent of investigation. For researchers and managers aiming to investigate whole-watershed patterns of fish distribution and abundance, this requires trading high-effort, site-specific sampling with low-effort, extensive sampling of entire stream lengths (e.g., Dolloff et al. 1993; Torgersen et al. 2006). Unfortunately, extensive sampling methods may be most vulnerable to sources of estimation bias (e.g., habitat-mediated sampling efficiency) and imprecision (Rosenberger and Dunham 2005).

Single-pass sampling in the context of backpack electrofishing typically consists of moving upstream through all accessible areas within a site on a single sampling occasion. This technique is used for covering great distances of stream length and is often performed in a continuous manner, sampling every meter of stream between predetermined points. Although labor intensive, it is ideal for sampling fish in headwater streams, where fish presence may be limited to a few kilometers of stream and where representative reach approaches fail to capture variability in fish distribution or the importance of habitat features present throughout entire riverscapes (Fausch et al. 2002; Gresswell et al. 2006; Torgersen et al. 2006).

In this study, we validate single-pass backpack electrofisher sampling methods to provide information on low-effort sampling efficiency of juvenile coho salmon in headwater streams and ascertain potential sources of estimation bias. This study will determine how accurately single-pass estimates reflect fish abundance over the range of habitat conditions available in Little Susitna headwater systems. Catch data from similar habitats can then be calibrated to confidently estimate juvenile salmon abundance, which will dramatically increase available information on those populations and reduce the likelihood of erroneous conclusions as a result of sampling bias. Specifically, our objectives were to: (1) conduct closed-population mark-recapture techniques to estimate the abundance of juvenile coho salmon in 50 or 100 m stream reaches of mainstem tributaries; (2) measure habitat features of mark-recapture sample reaches that may affect sampling efficiency (e.g., habitat area, woody debris, undercut banks); (3) develop logistic regression models to estimate single-pass sampling efficiency based on habitat features; and (4) create models that approximate mark-recapture population estimates based on single-pass catch and habitat covariates.

2.3 Methods

2.3.1 Study region

The Little Susitna watershed drains over 160 km² in the Cook Inlet region of southcentral Alaska (Figure 1). It originates at the Mint Glacier on Montana Peak in the Talkeetna Mountains north of Palmer, Alaska and flows southwest for approximately 177

km, discharging into upper Cook Inlet approximately 21 km west of Anchorage and 11 km east of the mouth of the Susitna River. Small headwater streams (e.g., Nurse's, Swiftwater, Colter, and Mary's Creeks) within the upper Little Susitna drainage are high gradient (channel slope greater than 2%), first order systems known to contain juvenile coho salmon (Johnson and Weiss 2007); however, the extent to which these headwater streams are used by this life stage is unknown.

2.3.2 Sampling design

Stream segments were selected within previously established 200 m stream reaches to conduct mark-recapture events. Stream segments were delineated beginning at discreet habitat unit breaks or at hydraulic control points favorable for block net deployment (i.e., no undercut banks and woody debris) and proceeded upstream to a similarly favorable net deployment site in close proximity to the designated site length. To collect fish for the marked baseline population, 6.5 mm mesh stainless steel minnow traps were placed in slow water habitats (e.g., pools, stream margins, undercut banks) within the chosen stream segment before block nets were in place. Traps were soaked for 12–24 hours. We used minnow traps rather than electrofishing to capture fish for marking to minimize post-marking recovery time and prevent potential capture effects from electrofishing that would create bias in our mark-recapture estimates. All captured juvenile coho salmon were anaesthetized in a 1:10 clove oil–ethanol solution (Cho and Heath 2000) at a 25–50 mg of clove oil solution/L water concentration (Kennedy et al.

2007) and measured to the nearest mm fork length. All captured juvenile coho salmon were marked by soaking them in Bismark Brown dye at a concentration of 21 mg Bismark Brown /L water for 50 minutes (Gaines and Martin 2004). Battery operated portable aerators were used to maintain oxygen levels during the dye bath. Non-target species were kept in perforated live wells outside of the stream segment until instream sampling was complete.

Six and a half mm square mesh netting was used to block the stream segments fish movements and establish a closed population, a fundamental assumption of mark-recapture population estimates (Otis et al. 1978; Seber 1982). Block nets secured with T-post fencing and sand bags were regularly cleared of organic materials to prevent bed scouring and net failure. Sampled stream segments were approximately 100 m in length unless block net failure from organic material accumulation or bed scour was frequent. If this practice did not prevent failure, reaches were shortened to about 50 m, reducing time needed to sample the reach and thus the duration that block-nets were in the water. All marked fish were returned to the closed stream segment and redistributed near their relative locations of capture. A 2 h recovery period prior to recapture sampling was set to maximize recovery while minimizing escape potential and net failure (Peterson and Cederholm 1984; Temple and Pearsons 2006).

Electrofishing was used for recapture sampling. Prior to sampling with a backpack electrofisher (LR-24 electrofisher, Smith Root, Vancouver, WA), water

temperature and conductivity were recorded using a water quality sensor (YSI 85, YSI inc., Yellow Springs, OH) to calibrate electrofisher settings. Moving upstream, one electrofisher operator, two dip netters, and a bucket carrier sampled for marked coho salmon from within each closed stream segment by exposing all areas within the channel to electricity (Reynolds 1996; Dunham et al. 2009). Voltage, pulse, and frequency were adjusted to optimize catch, beginning with a 30-Hz DC pulse at 12% duty cycle (4 ms) and 220-280 V (Reynolds 1996; Dunham et al. 2009). Once a single-pass of a reach was complete, coho salmon were anaesthetized, measured to fork length and visually inspected for Bismark brown coloration.

For each stream segment, habitat unit type was recorded (pools, riffles, rapids, or cascades; Bisson 1982; Helm 1985; Hawkins et al. 1993), as was information for each habitat unit, including length, mean bank-full width, maximum depth, mean depth, length of undercut banks, dominant and subdominant substrate, and wood debris characteristics. The bank-full width measurements of each habitat unit were visually estimated based on actual measurements recorded on one out of every five or ten units (Dolloff et al. 1993). Substrate particles were assigned to an eight category Wentworth (1922) scale as modified by Cummins (1962). Dominant substrate was recorded as particles of a given size class occupying more than half of the total substrate area, determined through visual observation (Appendix 2.A). For each stream segment, woody debris greater than 10 cm in diameter and 1 m in length was counted, classified, and assigned class values along a six-category scale following Flebbe (1999).

2.3.3 Statistical analysis

Models of sampling efficiency included environmental factors identified as important in efficiencies of fish capture using electrofishing techniques (Reynolds 1996; Peterson et. al. 2004; Rosenberger and Dunham 2005). The response variable is single-pass sampling efficiency and was determined as

$$n_2 \,/\, \widehat{N}$$

where

$\widehat{N}$ = Chapman mark-recapture estimator;

n_2 = the number of fish captured in the second sampling period; a single-pass through the reach with the backpack electrofisher;

which provides the baseline estimate of fish abundance (Seber 1982; Rosenberger and Dunham 2005) and

$$\widehat{N} \;=\; \{[(n_1+1)(n_2+1)]/(m_2+1)\} - 1$$

where

n_1 = the number of marked fish;

m_2 = the number of marked fish recaptured.

Variances of the population estimates were approximated as in Seber (1982). Confidence levels (CL) for population estimates with large sample sizes (e.g., m_2 greater than 50) were determined using the normal approximation (Seber 1982):

$$\widehat{N} \pm \{Z_{(\alpha/2)}[\sqrt{(V\widehat{N})}]\}$$

where $z_{\alpha/2}$ is the (1-α/2) quantile of a standard normal distribution and a 95% CL is given by $\alpha = 0.05$. Confidence levels for population estimates with small sample sizes (e.g., m_2 less than 50) were determined using values provided by Chapman (1948; reproduced in Seber 1982) based upon values of m_2.

Explanatory variables consisted of environmental factors known to affect sampling efficiency, standardized to site length. The weighted average of dominant substrate was calculated by multiplying the substrate category numerical value by the length of each habitat unit within a given reach, summed and divided by the total reach length and rounded to the nearest whole number. Wood pieces of size classes A and B, and C and D, respectively, were summed and divided by the total reach length to determine an average number of wood pieces per meter of stream reach for each grouped size class (Table 1 and Appendix 2.A). Lengths of undercut banks were determined as the total length of right- and left- undercut streambank as measured within a given reach. Mean cross sectional areas of each reach were determined by multiplying estimated widths, calibrated with actual measurements of stream width, and an average of depth for each habitat unit within a given reach. Calibrations to estimate width measurements were determined using the Basinwide Visual Estimation Technique (Dolloff et. al. 1993). The

cross sectional value for all habitat units within a given reach were summed and divided by the total number of habitat units within that reach. Mean fish length was determined by averaging fork lengths from among all juvenile coho salmon captured in a given reach.

2.3.4 Evaluation of site-scale correlates of sampling efficiency

A general linear modeling approach was used to explore relationships between environmental variables and single-pass sampling efficiency. The variables that best explained variability in sampling efficiency were selected using an information-theoretic approach (Burnham and Anderson 2002) as follows. First, a global model was constructed based on information from previous studies to select site-scale features that were most likely to have an effect on sampling efficiency (Table 1). Second, subsets of the global model were constructed as alternative candidate models. Variables known to affect sampling efficiency were distributed into three groups; mean cross-sectional area as a measure of stream size, instream cover, and fish size (Rosenberger and Dunham 2005). Instream cover included counts of instream wood and undercut bank length, and mean fish size was used as a metric of fish size. It was anticipated that sampling efficiency would decrease with stream size and cover and increase with average fish size. The global model was examined for goodness-of-fit and violations of model assumptions (e.g., residual patterns, homoscedasticity, normality, outliers). If the global model was found to be significant, the best approximating model (among candidate models) most

consistent with the data was selected using Akaike's information criterion (AIC; Akaike 1973), corrected for small-sample bias (AIC_c; Burnham and Anderson 2002). All statistical analyses were performed in R v 2.13.1 statistical programming language (R Development Core Team 2011).

Formal diagnostics and tests for violation of model assumptions included the Spearman's Rank correlation coefficient matrix, Durbin-Watson test for autocorrelation, Breusch-Pagan test for equal variance, RESET test for linear model assumption, Variance Inflation Factor (VIF) for variable covariance, and the Shapiro-Wilk test for normality. These tests were implemented using the R packages 'lmtest' (Zeileis and Hothorn 2002), 'car' (Fox and Weisberg 2011) and 'Hmisc' v3.8-3 (Harrell 2010).

2.3.5 Direct calibration of single-pass catches

Single-pass catches were used to predict mark-recapture population estimates for calibration. Mark-recapture estimates ($\widehat{N}$) were assumed to be proportional to the single-pass estimates (n_2). Because variability in the mark-recapture estimates increases with population size, we assumed a multiplicative error structure, resulting in the following model:

$$\widehat{N} = a \cdot (n_2)^{\beta} \cdot e^{\varepsilon}$$

where a and β are proportionality parameters that allow the mark-recapture estimates to increase more slowly ($\beta < 1$) or faster ($\beta > 1$) than the single-pass estimates and ε are

normally distributed errors with mean zero and variance σ^2. The model can be log-transformed by taking the natural logarithm of both sides of the equation to yield a simple linear regression model of the form:

$$\ln \widehat{N} = \alpha + \beta \ln(n_2) + \varepsilon \qquad \text{(Eq. 1)}$$

where $\alpha = \ln(a)$ and the errors are additive and normally distributed ($\varepsilon \sim N\{0,\sigma^2\}$). The model was fit using least-squares regression and the fit was examined for residual patterns, homoscedasticity, normality, and outliers to check model assumptions.

To evaluate how well the single-pass estimates predict the mark-recapture estimates, we computed the mean relative error (MRE) between the back-transformed abundances predicted from the calibration model ($\widehat{\widehat{N}}$) and the mark-recapture estimates ($\widehat{N}$) using leave-five-out cross-validation:

$$MRE = \frac{1}{R \cdot 5} \sum_{i=1}^{R} \sum_{j=1}^{5} \left| \widehat{\widehat{N}}_{i,j} - \widehat{N}_{i,j} \right| / \widehat{N}_{i,j}$$

where the model (Eq. 1) was fit R times to 22 randomly selected reaches ("training set") to predict abundances for the remaining 5 reaches (j = 1,2,…5) and back-transformed predicted abundances ($\widehat{\widehat{N}}$) were computed from the predicted log-abundances ($\widehat{\ln N}$) using a bias correction for the mean of a log-normal distribution (e.g. Sprugel 1983):

$$\widehat{\widehat{N}} = e^{\widehat{\ln(N)} + \hat{\sigma}^2/2}$$

$$\widehat{\ln N} = \hat{\alpha} + \hat{\beta} \cdot \ln(n_2)$$

where $\hat{\alpha}, \hat{\beta}, \text{and } \hat{\sigma}^2$ are the estimated parameters and residual variance from the fitted regression model (Eq. 1).

2.4 Results

2.4.1 Site-scale correlates of sampling efficiency

Population estimates and sampling efficiencies based upon $n = 27$ mark-recapture stream segments are listed in Table 2. Spearman's rank correlation coefficient revealed strong covariance among habitat variables; redundant variables, weighted average dominant substrate and wood size class F, were then removed from the global model (Appendix 2.B). The resultant global model met all formal tests for violation of model assumptions, including tests for autocorrelation, equal variance, linearity, normality, and variance inflation. The global model was not significant at the 95% confidence level (R^2 = -0.0018, *p*-value: 0.447), and all parameter estimates other than the intercept contained zero in their 95% confidence intervals (Table 3). The lack of significance of the global model indicated that sampling efficiency was not significantly affected by any of the habitat variables considered here. Therefore, calibration using single-pass catches only would be appropriate to adjust single-pass catches to reflect high-effort estimates of fish abundance.

2.4.2 Direct calibration of single-pass catches

A linear model of log-transformed first-pass catch of juvenile coho salmon performed well as a predictor of log-transformed mark-recapture abundance estimates (R^2

= 0.95, $p < 0.001$, Figure 2; Table 4). The 95% variability explained in the mark-recapture estimates pertains to the log-scale only, and does not reflect back-transformed abundance estimates. The mean relative error for predicting abundances was estimated to be 24.4%; therefore, with a 'training data set' of 22 reaches, the single-pass estimator produces an estimate that is about 24% lower or higher than the mark-recapture estimate on average, while the mean absolute error was approximately 111 fish (Figure 3). Of the 27 stream segments, thirteen mark-recapture estimates fell within 95% confidence intervals of the single-pass model predictions (Figure 4).

2.5 Discussion

Our validation exercise revealed that catch per unit effort from single-pass electrofisher sampling may be used as an index of abundance in headwater streams of the Little Susitna. Using sampling efficiency and mark-recapture abundance baselines, we developed a predictive model of relative abundance based upon single-pass catch of juvenile coho salmon (Figure 2). These findings are similar to other studies that used electrofishing methods to determine abundance estimates. For example, Riley and Fausch (1992) and Kruse et al. (1998) determined that complex in-stream habitat (e.g., undercut banks or woody debris) or variance in measures of stream size had a negligible effect on estimates. Riley and Fausch (1992) attributed this to thorough, non-time constrained sampling, rather than a constant unit of time as a measure of sampling effort. Because of our varied stream lengths, we could not standardize to time, and, similar to

Riley and Fausch (1992), a thorough sampling technique was used. Similar to Kruse et al. (1998), low variance in habitat conditions throughout our sites may have concentrated fish in discrete areas of habitat complexity within the reach. Although Kruse et al. (1998) included stream width in their model to account for additional variance in the relationship between single-pass electrofisher sampling and multiple-pass depletion population estimates (R^2 = 0.94 and 0.96 respectively), they concluded that no stream attributes were needed to strengthen the relationship. However, this is contrary to findings of other studies that have cited habitat complexity as factors that bias sampling efficiency (Kennedy and Strange 1981; Peterson and Cederholm 1984; Riley and Fausch 1992; Rodgers et al. 1992; Peterson et al. 2004; Rosenberger and Dunham 2005).

The use of two netters dedicated to netting stunned fish may have greatly reduced any habitat- or user-induced capture bias. For example, Jones and Stockwell (1995) incorporated two netters with a high correlation between single- (and multiple-) pass mark-recapture depletion population estimates, concluding, however, that single-pass catch of trout provided a consistent predictor of the population, but cautioned against the accuracy of the estimate. We were able to address this concern by incorporating accuracy into our predictive model through the cross-validation approach, thus providing accurate and precise population estimates.

We determined that, in streams with a narrow range of habitat conditions and low fish densities, single-pass electrofishing can accurately reflect abundance of fish,

assuming that our mark-recapture estimates are unbiased. This model may apply to similar headwater streams or other watersheds or geographic areas within the Matanuska-Susitna region that contain equivalent habitat conditions. However, we must caution that managers remain aware of the hazards of applying this model to estimate fish abundances in streams with habitat conditions beyond the range for which the model was developed. Failure to determine the effects of habitat-mediated biases may lead to inaccurate population estimates. Although labor intensive, validation is a useful tool for managers to assess population abundances of salmonids especially where entire stream extents are sampled in a continuous manner.

As shown with this study, low-effort sampling can approximate actual fish numbers without accounting for habitat covariates that could affect sampling efficiency; but the real advantage to this approach exists when addressing ecological processes operating on spatial scales equivalent to, or greater than, the stream segment level. For example, managers addressing longitudinal distributions of fish within headwater streams may wish to incorporate a low effort sampling approach, as it allows sampling over greater distances and in shorter time periods. This is in lieu of intensive sampling, which may yield more precise abundance estimates but is more costly in terms of time and effort. However, as no single scale is appropriate for investigating all ecological problems, special attention should be paid to the scale at which the process of interest occurs (Frissell et al.1986, Wiens 2002). Thus, it follows that a chosen sampling method

must be commensurate with research goals, and logistical, financial, and temporal constraints.

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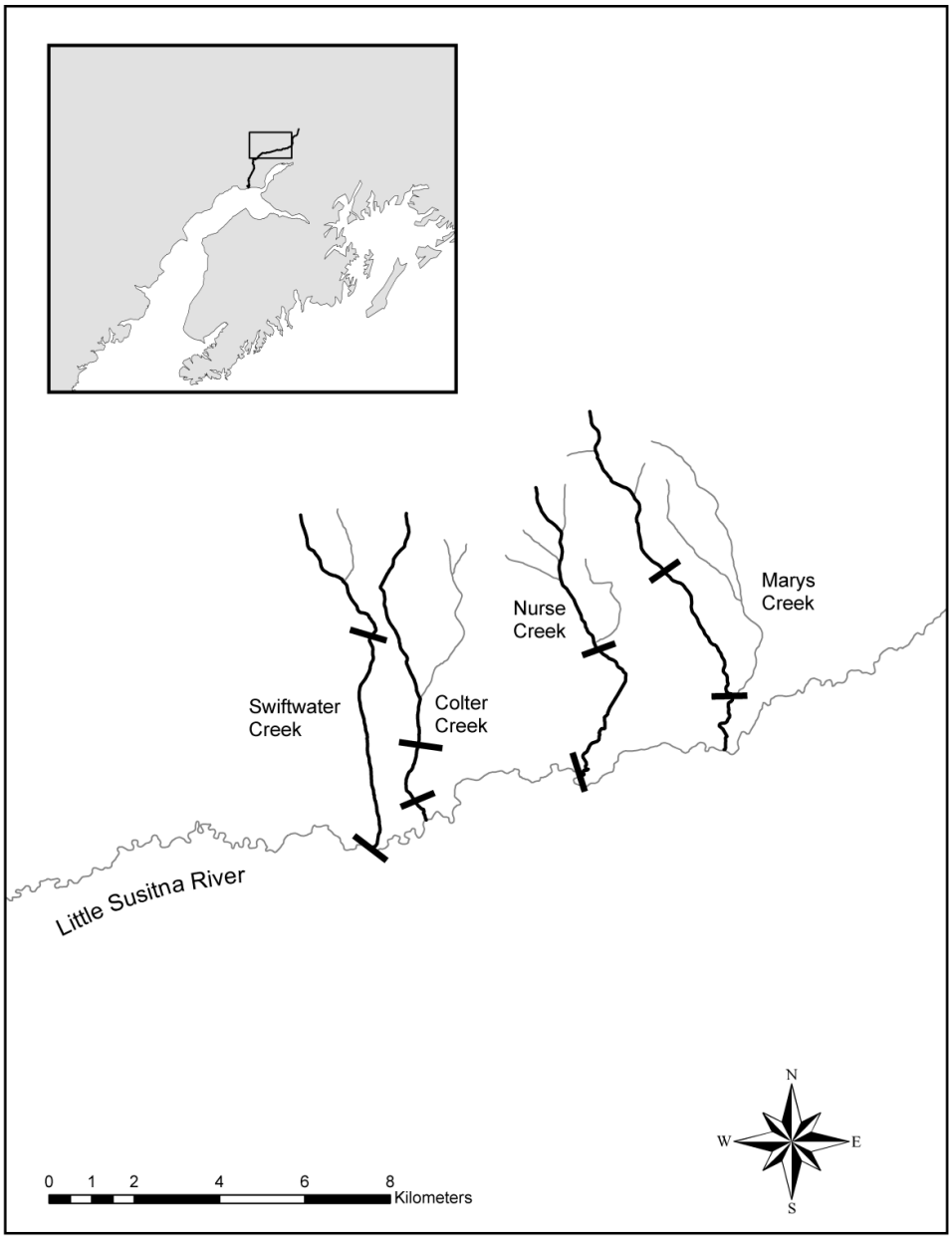

Figure 2.1 Study area map. Headwater streams of the Little Susitna River, Alaska, selected for mark recapture study during summer 2011. Line markers on the streams indicate the upper and lower boundaries of the study areas.

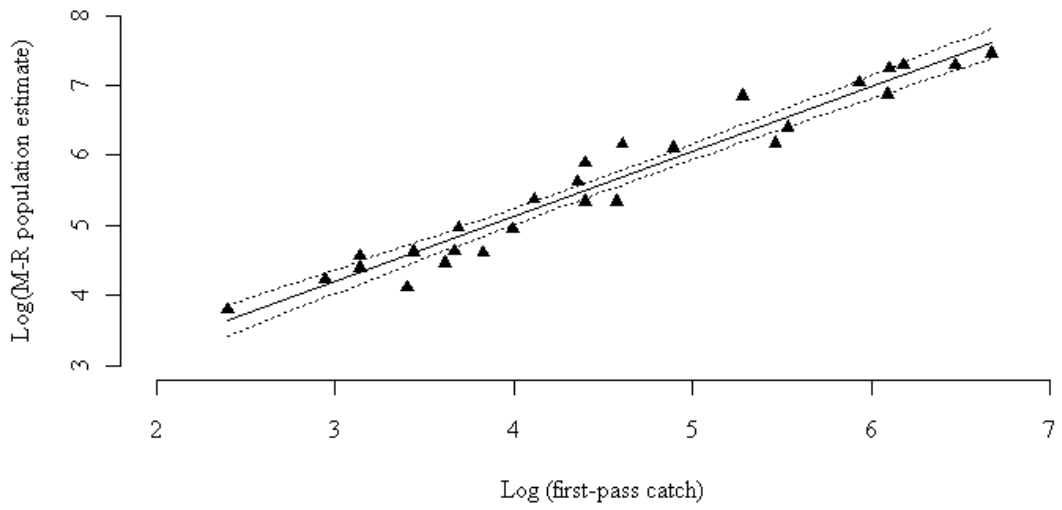

Figure 2.2 Mark-recapture population estimates as a function of single-pass catch. Natural log of mark-recapture population estimates as a function of natural log single-pass catch of juvenile coho salmon ($R2 = 0.95$, $p < 0.001$). Fish were sampled within headwater streams of the Little Susitna River, Alaska in 2011 at 27 study sites. Dashed lines represent 95% confidence intervals for the mean. The 95% variability explained in mark-recapture estimates pertains to the log-scale only, and does not reflect back-transformed abundance estimates.

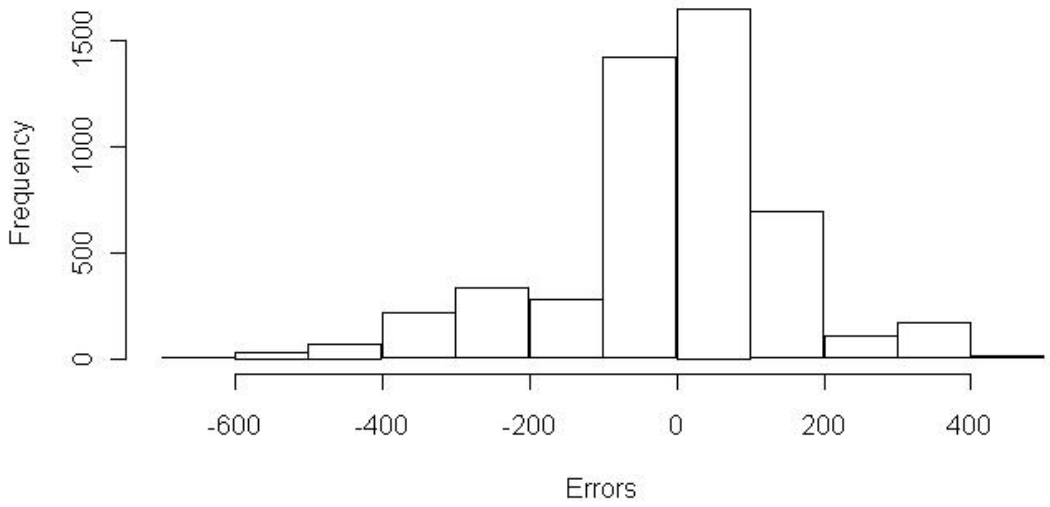

Figure 2.3 Error rate of predicted juvenile coho salmon abundances. Error in the number of fish (mark-recapture estimate of abundance minus single-pass predicted abundance expressed as error terms) associated with a bias- corrected back-transformation of predicted juvenile coho salmon abundances. Predictive models are on average off by approximately 111 fish (mean of absolute errors = 111).

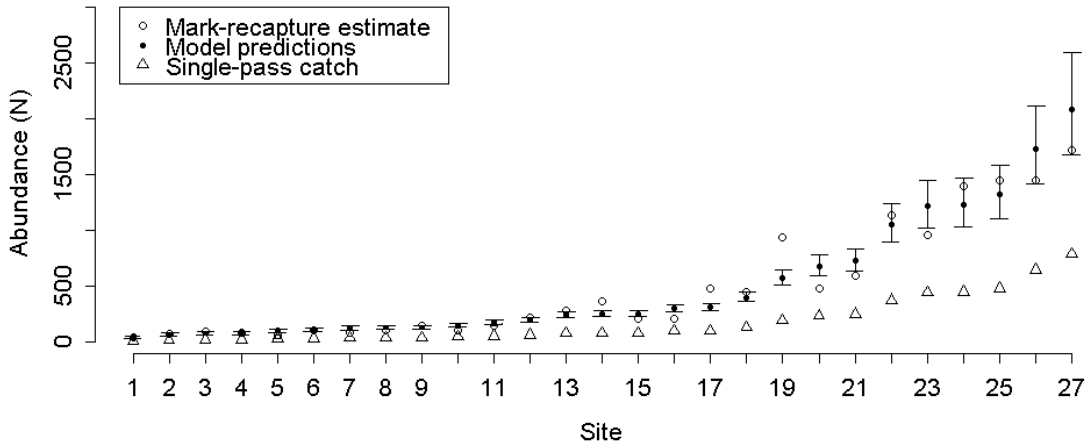

Figure 2.4 Model predictions of juvenile coho salmon. Abundance, first pass catch, and model predictions of juvenile coho salmon at 23 sites in headwater streams of the Little Susitna River, Alaska, sampled in 2011. Sites are ordered from lowest single-pass catch to highest. Vertical lines represent 95% confidence intervals of cross-validated model prediction estimates.

Table 2.1 Characteristics of study sites. Characteristics of (*n*=27) study sites located within four separate headwater streams of the Little Susitna River, Alaska, sampled to estimate juvenile coho salmon abundances in 2010-2011. Wood classes A-F represent size classes: 1 - 5 m in length (A) 10 - 50 cm diameter; (B) greater than 50 cm diameter, and greater than 5 m in length (C) 10 - 50 cm diameter; (D) greater than 50 cm diameter; rootwads; (E), and snags (clusters of wood pieces not of size class A-E; (F).

Variable	Abbreviation	Mean	SD	Range
Mean cross section (m^2)	CS	0.78	0.21	0.38—1.12
Site length (m)		83.2	25.4	51.8—134.8
Weighted avg. dominant substrate	DS	5.26	1.06	3.0—7.0
Total length undercut banks (m)	UB	31.69	14.67	5.0—68.0
Wood AB (#/m)	WAB	0.85	0.43	0.31—1.8
Wood CD (#/m)	WCD	0.08	0.06	0.00—0.19
Wood E (#/m)	WE	0.00	0.01	0.00—0.02
Wood F (#/m)	WF	0.06	0.03	0.02—0.13
Total coho salmon (#/ reach)		180	211	11—788
Mean fish size (mm)	MnFS	46.21	5.82	37.59—65.09
Fish (#/m)		2.11	2.76	0.11—11.04

Table 2.2 Population estimates from closed population marking periods. Juvenile coho salmon population estimates from closed population single marking period and single recapture period from 27 sites located within headwater streams of the Little Susitna River, Alaska, sampled in 2011. (n_1 = number caught and marked, n_2 = number caught in second sample period, m_2 = number marked juvenile coho in second sampling period, $\widehat{N}$= population estimator, **SD**= standard deviation of population estimator, LCL and UCL lower and upper confidence level respectively.)

n1	*n2*	*m2*	$\widehat{N}$	SD	95% LCL	95% UCL	Efficiency
98	100	20	475	80	294	758	0.21
52	40	14	144	24	79	252	0.28
136	133	40	447	48	320	614	0.30
47	377	15	1133	220	647	1967	0.33
62	235	30	479	56	324	692	0.49
33	97	15	207	34	117	355	0.47
36	788	16	1716	294	993	2894	0.46
43	81	9	360	90	172	756	0.23
25	441	11	957	192	488	1819	0.46
27	78	7	276	74	118	651	0.28
31	31	9	101	21	48	209	0.31
30	19	8	68	14	30	146	0.28
51	23	12	95	15	49	172	0.24

Table 2.2 (continued)

n1	*n2*	*m2*	$\widehat{N}$	SD	95% LCL	95% UCL	Efficiency
22	37	9	86	17	40	177	0.43
21	30	10	61	10	29	118	0.49
62	481	20	1445	246	896	2305	0.33
37	196	7	935	271	407	2241	0.21
32	81	12	207	40	109	381	0.39
22	54	8	140	32	62	304	0.39
17	39	6	102	26	40	257	0.38
16	23	4	81	25	25	272	0.29
41	61	11	216	46	111	413	0.28
31	46	14	99	15	54	173	0.46
183	645	81	1449	111	1232	1666	0.45
84	252	35	596	69	417	838	0.42
155	446	49	1394	152	1036	1860	0.32
18	11	4	45	12	14	146	0.25

Table 2.3 Sampling efficiency global model parameter estimates. Parameter estimates and 95% CL for predictor variables of the global model for determining sampling efficiency based on (n=27) mark-recapture sites within headwater streams of the Little Susitna River, Alaska sampled during 2011 (LCL = lower confidence limit; UCL = upper confidence limit).

Parameter	Estimate	Std. Error	95% LCL	95% UCL
Mean cross section	-1.14×10^{-1}	1.13×10^{-1}	-3.36×10^{-1}	1.08×10^{-1}
Length undercut bank	8.82×10^{-5}	1.25×10^{-3}	-2.36×10^{-3}	2.54×10^{-3}
Wood size class ab	-3.36×10^{-2}	4.87×10^{-2}	-1.29×10^{-1}	6.19×10^{-2}
Wood size class cd	-1.84×10^{-1}	3.68×10^{-1}	-9.05×10^{-1}	5.38×10^{-1}
Mean fish size	-6.89×10^{-3}	4.15×10^{-3}	-1.50×10^{-2}	1.25×10^{-3}

Table 2.4 Parameter estimate for best-fitting logistic regression model. Parameter estimate for best-fitting logistic regression model of mark-recapture population estimates based on known numbers of marked coho salmon released into a site and single-pass catch of coho salmon. Sites were located in headwater streams of the Little Susitna River, Alaska, and sampled in 2011 (CL = confidence limit).

Parameter	Estimate	95% LCL	95% UCL
Intercept	1.42	1.00	1.84
ln(single-pass catch)	0.93	0.84	1.02

Appendix 2.A

Size classification for substrate and wood pieces. Size classifications for categorizing substrate and wood pieces within stream reaches of headwater streams, Alaska.

Size classification		Diameter (mm)	Length (m)
Substrate			
	9 – Bedrock	Uniform	
	8 – Boulder	> 256	
	7 – Cobble	64 – 256	
	6 – Large gravel	10 – 64	
	5 – Small gravel	1.0 – 10	
	4 – Sand	0.061 – 1.0	
	3 – Silt	0.0039 – 0.061	
	2 – Clay	< 0.0039	
	1 - Organics	Various	
Wood			
	A	100 – 500	1 – 5
	B	> 500	1 – 5
	C	100 – 500	> 5
	D	> 500	> 5
	E	rootwads*	variable
	F	clusters**	< 1

* Rootwad not defined by diameter but presence of root structures
**Small pieces of wood as not described above, but contribute to habitat complexity.

Appendix 2.B

Spearman's correlation matrix of all-aged predictor variables. Spearman's rank correlation matrix of variables for inclusion into the global model. Row headings from left to right are; mean cross section, CS; weighted average dominant substrate, DS; wood AB, WAB; wood CD, WCD; wood E, WE; wood F, WF; and mean fish size, MnFS. Wood classes A-F represent size classes: 1 - 5 m in length (A) 10 - 50 cm dia.; (B) greater than 50 cm dia., and greater than 5 m in length (C) 10 - 50 cm dia.; (D) greater than 50 cm dia., rootwads; (E), and snags (clusters of wood pieces not of size class A-E; (F).

	Variables							
	CS (m^2)	DS	UB	WAB (#/m)	WCD (#/m)	WE (#/m)	WCD (#/m)	MnFS (mm)
CS (m^2)	1.00							
DS	0.50	1.00						
UB (m)	0.11	-0.17	1.00					
WAB (#/m)	-0.38	-0.66	0.09	1.00				
WCD (#/m)	0.14	0.15	0.01	-0.19	1.00			
WE (#/m)	0.46	0.35	0.11	-0.35	0.08	1.00		
WF (#/m)	-0.37	-0.33	0.04	0.63	-0.35	-0.36	1.00	
MnFS (mm)	-0.30	-0.01	-0.20	-0.17	0.31	-0.12	0.04	1.00

Chapter 3: Longitudinal patterns of juvenile coho salmon distribution and abundance in headwater streams of the Little Susitna River, Alaska[1]

3. 1 Abstract

Headwater streams are significant contributors to the diversity of life in river systems, and understanding their relative contribution to salmon production is vital for informed fisheries management and conservation. The role of headwaters as rearing habitat for juvenile coho salmon *Oncorhynchus kisutch*, and how habitat configurations within these areas support or limit coho salmon populations are poorly understood. To address these issues, we used a spatially continuous sampling approach to investigate distribution and abundance patterns of juvenile coho salmon cohorts within headwater streams of the Little Susitna River, Alaska and related these patterns to local, landscape and biological variables. Coho salmon were continuously distributed along the length of stream occupied, and that upstream limits varied up to 22 m in elevation between project years. Elevation and percent slope were consistent for describing upstream distribution limits. Age-1+ coho salmon were only 2% of all fish captured and exhibited a patchy distribution. Both elevation and weighted average dominant substrate were negatively

[1]Foley, K.M., A.E. Rosenberger, and F.J. Mueter. 2014. Longitudinal patterns of juvenile coho salmon distribution and abundance in headwater streams of the Little Susitna River, Alaska. Prepared for submission in North American Journal of Fisheries Management.

related to juvenile abundance in habitat models, suggesting female nesting habitat strongly affected current abundance of salmon in these systems. No clear or biologically meaningful relationships emerged for age-1+ fish. Although the headwater streams represented in our study are unlikely to produce numbers of coho salmon comparable to low gradient and side channel habitats downstream, it does not follow that peripheral habitats like these should be ignored in ongoing management and conservation efforts in the region; however, potential stream length occupied, with consideration of some landscape factors, may be all that is required for prioritization of headwater streams for restoration purposes.

3.2 Introduction

The ability to predict fish distributions and understand habitat factors that limit persistence is important for informed fisheries management and conservation. Assessment of habitat suitability and estimation of habitat loss due to disturbance can indicate which habitat configurations are most limiting or productive for a given species at a selected scale (Orth and Maughn 1982; Moyle and Baltz 1985; McClendon and Rabeni 1987; Orth 1987). Habitat models that predict the occupancy of a species at reach and watershed spatial scales over one to ten year time periods are typically of most interest to managers because manipulations, like stream bank stabilization or stream corridor restoration are not only relevant to fish populations, but also logistically and socially feasible (Fausch et al. 2002).

When managing a fish species that requires discrete habitats for completion of its life history, understanding the principles of landscape complementation and supplementation will provide important insight for conservation and management (Tilman 1982; Frissell et al. 1986; Dunning et al. 1992). For example, the presence of resources associated with summer rearing habitat patches, complemented by the close proximity of favorable, relatively ice-free, overwintering patches, enables a region to support salmonid (*Oncorhynchus spp.*) populations (Peterson 1982, Nickelson et al. 1992). Core areas of production may provide ideal habitats for certain life history stages, reflected in high numbers of individuals; however, if any of these habitats become unavailable or saturated, peripheral areas, such as headwater streams, can serve a supplemental role by providing alternative areas for rearing, overwintering, or refugia, leading to greater resilience of populations to catastrophic or temporary disturbance (Rieman and Dunham 2000, Roghair et al. 2002). If we neglect to sample and account for these peripheral habitats, or sample them sporadically in space and time, their functional importance may be underestimated. Further, a continuous view of these habitats in either space or time provides additional insight that would otherwise be lacking in a more piecemeal or reach-specific study (Gresswell et al. 2006).

A wide variety of habitat features are important for rearing and growing salmonids in headwater streams (Fausch et al. 1988). These include features related to salmonid growth such as macroinvertebrate productivity (Richardson 1993), water

velocity (Bisson et al. 1988), and thermal regimes (Welsh et al. 2001). Other important features for the long-term survival and persistence of fish species include measures of habitat complexity such as the presence of wood debris (Fausch and Northcote 1992; Crispin et al. 1993), habitat surface area (Burns 1971), and pool frequency (Dolloff 1986). Despite this potential value for rearing, research suggests juvenile coho salmon *O. kisutch* are not found in their highest abundances in these habitats, preferring instead slow-velocity areas, including backwaters, floodplains, oxbow lakes, upland sloughs, beaver ponds, and a variety of off-channel habitats (Murphy et al. 1989; Bjornn and Reiser 1991; Collins et al. 2003; Pollock et al. 2004) rather than higher gradient headwater streams. Areas of low water velocity allow fish to optimize their energy budgets by allocating greater amounts of energy towards growth and development rather than maintaining a constant swimming position in the water column (Quinn 2005). This trade-off and allocation of energy resources allows them to attain a larger body size during their early life stages, improving survival (Werner and Gilliam 1984; Quinn and Peterson 1996). Additionally, the high surface area to shoreline ratio associated with backwaters results in a greater quantity of shallow-water habitat. These areas often contain emergent vegetation that provides cover from predators, and shallow margins warm quicker during summer periods than open water areas, enhancing juvenile coho salmon growth if sufficient food is available.

Slow-water habitats are often where juvenile coho salmon are found at their highest densities (core areas); however, backwaters and side-channels are not the only

habitat-type occupied during this crucial life stage. The relative contribution of peripheral habitat, such as high-gradient headwaters or estuaries, to salmon production is unknown. Juvenile coho salmon will take up position and defend territories in suitable areas of the stream channel (Quinn 2005), yet, during times of high abundance, fish unable to defend territories may move to alternate rearing habitats. For example, after emergence from the gravel in April – June, a large number of fry may move downstream as "nomads", a term first used by Chapman (1962), giving rise to the concept of surplus fry. These fry exhibit a high degree of plasticity in habitat selection during early life stages; peripheral habitats may fulfill a critical complementary or supplementary role providing nursing and rearing areas for these individuals. For example, juveniles can use estuarine environments in the event of freshwater habitat saturation during their first year of life (Hoem-Neher et al. 2013). Koski (2009) proposed this behavior as a life-history strategy coho salmon use to take advantage of more productive diverse habitat opportunities located downstream in estuarine environments.

Fish experiencing density-dependent processes in side-channel habitats may also move upstream to find alternative or supplementary rearing habitat. Although coho salmon are frequently documented in headwater streams (Johnson and Weiss 2007), we are not aware of any work documenting the use of, or relative contribution of, headwater streams as rearing areas for juvenile coho salmon, particularly in southcentral Alaska, where our study was based. These high gradient (e.g., >2% slope) headwater streams provide habitat features consistent, if not optimal, with the needs of juvenile coho salmon

for completion of different life stages and have potential for playing this role (Rosenfeld et al. 2000).

In this study, we determined longitudinal distribution patterns of juvenile coho salmon by age and size class within headwater streams of the Little Susitna drainage, southcentral Alaska, and associated spatial patterns in juvenile fish distributions with local and landscape scale habitat features. This study will help elucidate the extent to which juvenile coho salmon use these areas as rearing and nursery habitats and provide area managers with a greater understanding of early life history and habitat use by juvenile coho salmon. An understanding of the relative value of these habitats could provide managers with important information regarding restoration of fish passage through culvert replacement for roads crossing these headwater streams.

3.3 Methods

3.3.1 Study region

The Little Susitna watershed drains over 160 km² in the Cook Inlet region of southcentral Alaska (Figure 1). It originates at the Mint Glacier on Montana Peak in the Talkeetna Mountains north of Palmer, Alaska and flows southwest for approximately 177 km, discharging into upper Cook Inlet approximately 21 km west of Anchorage and 11 km east of the mouth of the Susitna River. Small headwater streams (e.g., Nurse's, Swiftwater and Mary's Creeks) within the upper Little Susitna drainage are high gradient

(channel slope >2%), single order systems known to contain juvenile coho salmon (Johnson and Weiss 2007).

3.3.2 Sampling design

During 2010 and 2011, juvenile coho salmon were sampled within three headwater streams of the Little Susitna River to the upstream extent of their distribution (Figure 1). Sampling within Nurse's Creek occurred during 2011. Sampling occurred between the June-October growing and feeding period. Prior to sampling, crews delineated continuous stream reaches of approximately 200 m in length, beginning at the confluence with the mainstem and continuing upstream to approximately 400 m in elevation. Reaches ended at discreet habitat unit breaks formed from distinct hydraulic control points. Within Mary's Creek, delineation of stream reaches and distribution sampling began at approximately river kilometer (rkm) 0.8 (measured from its confluence with the Little Susitna River) due to the presence of a tributary junction. We delineated stream reaches throughout the entire stream course in a continuous manner, thus, the upstream boundary of one reach served as the downstream boundary for the next (Dolloff et al. 1993).

Water temperature and conductivity were recorded using a water quality sensor (YSI 85, YSI inc., Yellow Springs, OH) to calibrate electrofisher settings prior to sampling with a backpack electrofisher (LR-24 electrofisher, Smith Root, Vancouver,

WA). Moving upstream, one electrofisher operator, two dip netters, and a bucket carrier sampled for coho salmon from within each stream reach by exposing all areas within the channel to electricity (Reynolds 1996; Dunham et al. 2009). Voltage, pulse, and frequency were adjusted to optimize catch, beginning with a 30-Hz DC pulse at 12% duty cycle (4 ms) and 220-280 V (Reynolds 1996; Dunham et al. 2009). Once a single-pass of a reach was complete, coho salmon were anaesthetized and measured to fork length.

We collected scales from a subset of all captured individuals to corroborate the age structure of juvenile coho salmon within the study area inferred from length frequencies. Scale samples collected in the field followed the procedures outlined by Jerald (1983) and aged using the standards and guidelines of Mosher (1968). For analyses, scales were mounted on glass slides and viewed on a laboratory microscope and photographed (Table 2).

In 2010, we determined the upstream spatial limit to sampling by catch rate of juvenile coho salmon. If we failed to catch coho salmon in two consecutive stream reaches, sampling ceased, and the reach where the last fish in hand occurred was designated as the upper limit of their distribution. To assess changes in upstream distribution, we engaged in repeat sampling at reaches designated as the upper extent. We resampled the upper reaches once during July, August, and September in 2011. If fish were captured within the predetermined stream reach, crews continued to sample upstream until two consecutive reaches resulted in zero coho salmon catch. If no coho

salmon were captured within the reach, crews moved to the beginning of the first reach located immediately downstream and began sampling upstream, repeating the pattern until a minimum of two juvenile coho salmon were captured.

Throughout each stream reach, we recorded habitat units as being pools, riffles, runs, or cascades (Bisson et al. 1982; Helm 1985; Frissell et al. 1986; Hawkins et al. 1993). Within each habitat unit, we recorded its length, mean bank-full wetted-width, maximum depth, mean depth, length of undercut banks, dominant and subdominant substrate, and wood debris characteristics. The bank-full wetted-width measurement of each habitat unit was visually estimated with actual measurements recorded for one out of every five units (Dolloff et al. 1993). Substrate particles were assigned to an eight category Wentworth (1922) scale as modified by Cummins (1962) and recorded moving upstream through each habitat unit. We recorded "dominant" substrate as particles of a given size class occupying more than half of the total substrate area, determined through visual observation. For each stream segment, we counted and classified woody debris greater than 10 cm in diameter and 1 m in length and assigned class values along a six-category scale following Flebbe (1999). To determine elevation and percent slope values, 2M rasters were derived using 1:24,000-scale topographic maps and the spatial analyst extension in ArcGIS Service pack 1 (ESRI, 2010).

Spatial variation of stream temperature was monitored beginning June 2010 through September 2011, using temperature data loggers (UTBI-001 HOBO TidbiT v2

Temp Loggers, ONSET, Pocaset, MA) spaced at 400 m intervals within each stream (Dunham et al. 2005). In addition to 400 m intervals, data loggers were placed above and below hydrologic features (e.g. beaver ponds, tributary confluences, wet meadows) to help identify temperature variability within these areas. Prior to instream deployment, all temperature loggers were calibrated using the ice-bath technique and set to a 1-hour sampling period to reduce the error rate of missing the true maximum / minimum diel temperature within each reach to less than two percent (Dunham et al. 2005).

3.3.3 Statistical analysis

Models of juvenile coho distribution and abundance included local and landscape scale features identified as important for supporting salmonid populations (Fausch et al. 1988, Rosenfeld et al. 2000). The response variable is single-pass catch abundance estimate, calibrated using a linear model of log-transformed first-pass catch of juvenile coho salmon (See Chapter II), and standardized to 100 m stream lengths. Single-pass calibrated abundance estimates were divided by the total stream reach length, and multiplied by 100 m to standardize single-pass calibrated abundance estimates for each reach. Standardizing single-pass calibrated abundance estimates was necessary given the range of stream reach lengths (Table 1) and are referred hereafter as calibrated abundance estimates.

Explanatory variables consist of environmental factors documented within the literature to have influence on coho salmon distributions; site scale variables were standardized to reach length. A list of explanatory variables and abbreviations used throughout the remainder of this manuscript are included in Table 1. The weighted average of dominant substrate (DS) was calculated by multiplying the substrate category numerical value by the length of each habitat unit within a given reach, summed and divided by the total reach length and rounded to the nearest whole number. Wood pieces measured in the field were grouped together for analysis based upon diameter requirements; wood pieces of size classes A and B (WAB), and C and D (WCD) were summed together and divided by the total reach length to determine an average number of grouped, sized class pieces per meter of stream reach. Lengths of undercut banks (UB) were determined as the total length of right- and left- undercut streambank as measured within a given reach. Mean cross sectional areas (CS) of each reach were determined by multiplying estimated widths, calibrated with actual measurements of stream width, and an average of depth for each habitat unit within a given reach. Calibrations to estimate width measurements were determined using the Basinwide Visual Estimation Technique (Dolloff et. al. 1993). The cross sectional value for all habitat units within a given reach were summed, and divided by the total number of habitat units within that reach. Two meter rasters generated using ArcGIS Service pack 1 were used for determining elevation (EV) and percent slope (PS) values. The measure of percent slope for a given reach was determined as the difference in elevation between the upstream and downstream terminal points of that reach, divided by the total reach length.

The maximum daily average temperature (MDAT; ºC) for each logger was determined as a metric of stream temperature. An averaged maximum metric was selected as the mean temperature as it provides a good indicator of the overall thermal suitability and conditions for growth, whereas the maximum provided an indicator of temporary conditions associated with seasonal extremes (Dunham et al. 2005; Isaak et al. 2010). For each day, water temperatures recorded within the 24-hour period (designated as 12:00am to 11:59pm) were summed and averaged. Discarded from the analyses were days with fewer than 24 temperature measurements (tidbit malfunction or deployment/extraction day). The single highest average temperature was then selected for each tidbit as the representative metric value.

3.3.4 Evaluation of environmental conditions affecting distribution and abundance

We used a linear mixed-effects model and a linear model approach with general least squares to explore relationships between environmental variables and calibrated abundance estimates for all-aged and age-1+ juvenile coho salmon respectively. Using an information-theoretic approach (Burnham and Anderson 2002) for hypothesis testing and model selection, a global model was constructed based on information from previous studies to select site-and landscape scale features (Table 1) that were most likely to explain fish distributions. Candidate models were subsets of the global model. Variables within the global model were distributed into four main groups; maximum daily average

temperature as a metric of stream temperature, stream size, location in watershed, and instream cover. Stream size included channel connections, mean cross section, and total pool area, whereas location in watershed included elevation and percent slope. Instream cover included counts of instream wood pieces, undercut bank length, and weighted average of dominant substrate. The global model was examined for goodness of fit and violations of model assumptions (e.g., residual patterns, homoscedasticity, and normality of outliers). If the global model was found to be significant, the most likely candidate model was selected using Akaike's information criterion (AIC; Akaike 1973) corrected for small-scale sample bias ($AIC_{c;}$ Burnham and Anderson 2002). The most likely candidate model was selected from among all candidate subset models based upon a value of Δ_i less than or equal to four. If more than one candidate model emerged as the most likely candidate model, (i.e., a Δ_i, AIC difference between the 'first' and 'second' best approximating model is less than or equal to four), we incorporated a multimodel-based inference and averaging approach for parameter estimates (Burnham and Anderson 2002). All statistical analyses were performed in R v 2.13.1 statistical programming language (R Development Core Team 2011). Linear mixed effects models were implemented using the R packages 'nlme' (Pinheiro and Bates 2000). Explanatory variables were examined for multi-collinearity using a Spearman's Rank correlation coefficient matrix (i.e. values greater than or equal to, 0.60). Transformations to normalize data were assessed using the Box-Cox power transformation.

To evaluate how well landscape and local environmental variables predict calibrated single-pass catch abundance estimates, we used a linear mixed-effects model of the form:

$$Y_{i,j,k} = \alpha + \sum_p (X_{p,i,k} \cdot \beta_p) + b_k + \varepsilon_{i,j,k} \qquad \text{(Eq. 1)}$$

where $Y_{i,j,k}$ is the raw or transformed single-pass abundance estimate for observation i in reach j and stream k, β_p is a fixed effect of the p^{th} explanatory variable X_p, b_k is a random intercept for stream k to account for differences in mean catch rates among streams, which is assumed to be independent and normally distributed with mean zero and variance σ_b^2, and the errors $\varepsilon_{i,j,k}$ are additive and assumed to follow a multivariate normal distribution ($\varepsilon_{i,j,k} \sim N\{0, \sum_{j,m}\}$) with mean 0 and a variance-covariance structure Σ_{jm} in which the correlation between reaches j and m decreases exponentially with the geographic distance between them if j and m are in the same stream and is zero if j and m are in different streams. The model was fit using maximum likelihood and the fit was examined for residual patterns, homoscedasticity, normality, and outliers to insure model assumptions were met.

3.3.5 Model averaging

We incorporated a multimodel-based inference and averaging approach for parameter estimates based upon a 95% confidence set of models (Symonds and Moussalli 2011).

For fitted mixed effect linear models, we calculated a modified version of AIC (AIC_c) as:

$$\mathrm{AIC_c} = \mathrm{AIC} + \frac{2k(k+1)}{n-k-1}$$

where L is the log-Likelihood and k = model degrees of freedom or number of parameters and n is the number of observations. Comparisons were made for AIC scores as the difference between the best approximating model (lowest AIC_c) and all other AIC model scores (Δ_i). To assess the relative strength of each of the candidate models we determined evidence ratios (ER) and Akaike weights (w_i) based on the following equations (Burnham and Anderson 2002).

Akaike's weight (w_i)

$$w_i = \exp(-\frac{1}{2}\Delta_i) \Big/ \sum_{r=1}^{R} \exp(-\frac{1}{2}\Delta_r)$$

where R is the number of models and evidence ratio (ER) calculated as:

$$\mathrm{ER} = w_{i\_best}/w_i$$

where w_{i_best} corresponds to the (w_i) of the model with the lowest AIC value. Parameter estimates for each model contained within the 95% confidence set were determined as a weighted average:

$$\tilde{\tilde{\beta}} = \sum_{i=1}^{R} w_i \hat{\beta}_i$$

and the variance of parameter $\tilde{\tilde{\beta}}$ was estimated following Burnham and Anderson (2002; see also Lukacs et al. 2009):

$$\widehat{var}\left(\tilde{\tilde{\beta}}\right) = \sum w_i \left[\widehat{var}\left(\hat{\beta}_i\right) + \left(\beta_i - \tilde{\tilde{\beta}}\right)\right]$$

3.4 Results

3.4.1 Scale sample and length frequency analyses

Age analyses from *n* = 83 scale samples revealed a size threshold for age-0 and age-1+ juvenile coho salmon at 81 mm (Table 2; Appendix 3.1). Using the size threshold of 81 mm applied to our calibrated single-pass catch abundance estimates, we determined approximately 2% of all fish captured were age-1+ fish. Fork length histograms of temporal strata are unimodal with a right-skewed distribution and take into account growth over the sampling period (Figure 2; Appendix 3.2). The main peak within each histogram represents the central tendency of age-0 length distribution. The absence of pronounced secondary or tertiary modes in the right tail of the histogram obscured evidence for age-1+ cut-off values (Appendix 3.2).

3.4.2 Distribution of juvenile coho salmon – All-age fish

All-age juvenile coho salmon were continuously present in all stream reaches to their upstream distributional limits within Swiftwater and Mary's creeks (Figure 3). The discovery of an undocumented culvert pipe at approximately rkm 4.6 of Nurse's Creek prevented further upstream sampling within the stream, thus the upper distributional limits of juvenile coho salmon could not be determined. The maximum EV, DM, and PS values describing the uppermost extent of juvenile coho salmon distribution over the course of the study period were EV=289 m, DM=5,408 m, PS= 5%; EV=283 m, DM=5,290 m, PS=5%; EV=240 m, DM=4,422 m PS=5%, for Swiftwater, Mary's, and Nurse's creek, respectively (Table 3). The 2010 upper limit to distribution within Swiftwater Creek occurred at an EV of 289 m, an approximate distance of 5.4 rkm upstream from the confluence with the Little Susitna River. Within Mary's Creek, the upper limit of distribution occurred at EV 265 m, 4.8 rkm upstream of the confluence with the Little Susitna River. The PS within each of these reach areas correspond to 5%, compared to an average slope in both streams of 3% and 2% for Swiftwater and Mary's, respectively (Figure 3; Tables 3 and 4).

Repeat sampling of Swiftwater Creek in September 2010 revealed no change in the upper distribution limit for all-age fish. Repeat sampling in 2011 revealed a small decrease in the upstream distribution limits within Swiftwater Creek (EV=267 m; DM= 5.0 rkm) and a small increase in the upstream distribution limits within Mary's Creek (EV=283 m; DM=5.2 rkm) for all-age fish from 2010 (Table 4). Upstream limits of fish

distribution within Swiftwater and Mary's creeks remained constant through all months resampled during 2011 (Table 3).

3.4.3 Distribution of juvenile coho salmon – Age-1+

Fish greater than age-1 were found in 60%, 50% and 86% of all stream reaches sampled within Swiftwater, Mary's, and Nurse's creeks, respectively (Figure 4). The upstream extent for age-1+ fish within Swiftwater Creek occurred at an EV of 267 m, an approximate distance of 5 rkm upstream from the confluence with the Little Susitna River, with similar distributional trends shown for all-aged fish. Within Mary's Creek, the upper limit of distribution occurred at an EV of 238 m and a distance of approximately 4.2 rkm upstream of the confluence with the Little Susitna River. The PS within each of these reach areas correspond to 4% and 6% for Swiftwater and Mary's creeks respectively (Table 4). The upper limit of distribution for age-1+ fish accounts for approximately 92%, 79%, and 90% of the total stream length sampled in 2010 within Swiftwater, Mary's, and Nurse's creeks, respectively. Further, we found age-1+ fish occupied approximately 64%, 44%, and 89% of the habitat length sampled within Swiftwater, Mary's, and Nurse's creeks, respectively. No fish > age-1 were captured during repeat sampling within Swiftwater or Mary's creeks.

3.4.4 Environmental conditions affecting juvenile coho salmon – All-age fish

Calibrated single-pass catch abundance estimates for all aged juvenile coho salmon and environmental conditions were based upon $n = 69$ stream reaches. Spearman's rank correlation coefficients revealed strong covariance among habitat variables; redundant variables, maximum daily averaged temperature MDAT, total undercut bank UB, wood pieces size class AB and size class F WAB and WF, respectively and DM, were then removed from the global model; Appendix 3.3). Calibrated single-pass catch abundance estimates of juvenile coho salmon were square root transformed to meet normality assumptions.

A linear mixed-effects model was fit incorporating a random stream effect and exponential spatial structure within each stream. The exponential spatial structure is based on "units" (i.e., stream reach number), which approximates river distance between reaches and assumes a constant reach length of one. Variability among streams (SD 6.45; lower and upper 95% CI's; 2.67, 15.58), and variability within streams (SD 3.99; lower and upper 95% CI's; 2.99, 5.34) suggested greater variability among streams than within, and 95% confidence intervals suggest that between-stream variability is significantly larger than zero, hence the data were not pooled across streams. This statistical significance justified the use of the linear mixed effects model, which allows for random variability in counts of abundance among streams, which specifies our model intercept varies across streams. The estimated range of the exponential spatial covariance function suggests that observations are strongly autocorrelated up to a distance of approximately

217 m, compared to an average reach length of 205 m. The autocorrelation suggested that our stream reaches are similar to one another within 217 m of any one point.

3.4.5 Model selection – All-age

AICc rankings of the global model and subset candidate models suggested overwhelming support for a single candidate model. Based on overwhelming support for standardized calibrated single-pass catches, juvenile coho salmon abundance was predicted as:

$$\sqrt{\widehat{N_{juv\ coho}}} = 40.636 - 0.055(EV) - 2.31(DS) \qquad \text{(Eq. 2)}$$

where elevation (EV) and average weighted dominant substrate (DS) were predictor variables (Table 5).

Over the range of EV represented over our study sites (110.9 – 383.3 m), and DS held constant at the mean (6), we expect an effect of an absolute reduction of 396 juvenile coho salmon per reach from the lowest elevation to the highest elevation sampled. Similarly, over the range of DS represented over our study sites (4 – 8), and EV held constant at the mean (192.9 m), we expect an effect of an absolute reduction of 300 juvenile coho salmon from the smallest to largest substrate size (Table 6).

3.4.6 Environmental conditions affecting juvenile coho salmon – Age-1+

Calibrated abundance estimates for age-1+ juvenile coho salmon and environmental conditions were based upon *n*=69 stream reaches. Spearman's rank correlation coefficients revealed strong covariance among habitat variables; redundant variables, distance to mainstem, maximum daily averaged temperature, undercut banks, wood AB, and wood F, were then removed from the global model (Appendix 3.3). Incorporating a random effect and exponential spatial structure to capture differences in age-1+ calibrated fish abundance estimates among streams was minimal (SD<0.001) suggesting a fit with a linear model with autocorrelation using generalized least squares as more appropriate than fit with a linear mixed-effects model (AIC 177.70 and 179.70 respectively). The estimated range of the exponential spatial covariance function suggested that observations are strongly autocorrelated up to a distance of approximately 287 m on a single stream for age-1+ fish.

3.4.7 Model selection – Age-1+

AICc rankings of the global model and all model subsets did not reveal overwhelming evidence and support for a single candidate model of local and landscape correlates related to abundance of age-1+ juvenile coho salmon (Table 7). Among the full set of plausible models, four candidate models had accumulative AICc weights (acc *wi*) less than 0.95 for inclusion into the 95% confidence set of 'best-ranked' models for an averaged composite model. The AICc-averaged composite model of calibrated single-pass catch for age-1+ juvenile coho salmon predicted abundances as:

$$\ln \widehat{N_{age1+}} = 2.68 - 0.005(EV) + 0.007(PS) + 0.912(WCD) - 0.0.85(DS) + 0.023(CS),$$

where elevation (EV), percent slope (PS), wood pieces size class CD (WCD), weighted average of dominant substrate (DS), and mean cross-section (CS) were predictor variables (Table 8). In order of predictor weight, EV and PS had the highest probabilities (0.50) of being a component of the best model followed by WCD and DS with similar weights (0.38). The variable with the lowest predictor weight was CS (0.08). Among the variables within the AICc-averaged composite model, all contained zero within their 95% confidence intervals, suggesting insufficient evidence that age-1+ juvenile coho salmon were selecting for habitat configurations measured within this study (Table 8). All variables within the AICc-averaged composite model did not show sufficient evidence for an effect upon abundances; EV (estimate: -0.005, SE: 0.769), PS (estimate: 0.007, SE: 0.001), WCD (estimate: 0.912, SE: 3.96), DS (estimate: -0.085, SE: 0.085), and CS (estimate: 0.023, SE: 0.079).

3.5 Discussion

Our intent in this study was to examine the importance of headwater streams as rearing habitat for juvenile coho salmon in the Little Susitna River. Ongoing restoration activities within the Matanuska-Susitna region are primarily focused on juvenile passage

and providing access throughout these systems via replacement of barrier road culverts. Many of the remaining barriers to dispersal are primarily located in small, headwater streams, whose value to juvenile coho salmon remains unknown. Given that this species is known to prefer side-channel tributaries off mainstem river habitats (Hartman et al. 1987; Swales and Levings 1989; Murphy et al. 1989; Nickelson et al. 1992), headwater streams are likely peripheral to core, higher density, rearing areas. However, their use may allow for greater life history variability and provide supplemental habitat for the Little Susitna coho salmon population should density-dependent processes limit the number of individuals occupying core habitats. They also may play a complementary role if habitats become unavailable due to flooding or severe disturbance in mainstem core habitats. To assist with prioritizing culvert replacement, our goal was to determine the extent to which these habitats are used by juvenile coho salmon, including age-1+ individuals that are likely moving into the system from overwintering refugia, and age-0 individuals, who may either be using these areas for rearing and/or moving downstream from adult spawning locations to other rearing habitats off the mainstem river. We also examined what habitat features along the length of streams sampled were associated with increased abundance of juvenile coho salmon.

3.5.1 Distribution juvenile coho salmon – All-age fish

Juvenile coho salmon in headwater streams of the Little Susitna River were continuously distributed at the reach scale, along the length of stream occupied. The

upstream limits to their distribution ranged from 265 to 289 m in elevation and varied up to 22 m in elevation from year to year. This suggests that stream size, thermal conditions, or other correlates of elevation set the distribution limits in these streams, rather than natural barriers or abrupt changes in gradient (e.g., cascades). It is important to note that thermal regimes within headwater streams have been linked to good-fitting models of presence-absence of juvenile coho salmon (Welsh et al. 2001). Despite this evidence, we removed our metric of stream temperature (MDAT) from the modeling exercise in lieu of elevation because of the very strong negative correlation that exists between the two variables (Appendices 3.3 and 3.4). We do not wish to assert that elevation is driving the distribution of these fish; rather it may be that landscape patterns in habitat and stream features that covary with elevation are more important than local habitat conditions within the range of conditions of our study sites. However, similarity in elevational upstream limits among and within streams and over years suggests that, in the absence of manmade barriers or unusual geological formations, elevation may be used to estimate the upstream distributional limits of juvenile coho salmon, with the assumption that the entire length of stream below is occupied.

During 2010, the upper limit of distribution within Mary's Creek was determined in late September, towards the end of the summer growing period. Although timing of migration by juvenile coho salmon between summer rearing habitat and overwinter refugia is unknown for headwater stream environments of the Little Susitna, it is unlikely our sampling failed to capture the furthest upstream extent of distribution within this

stream. Observation of movements of juvenile coho salmon within Carnation Creek, British Columbia into off-channel, winter rearing habitats occurred during September-December (Bustard and Narver 1975; Hartman and Brown 1987). Further, repeat sampling within Mary's and Swiftwater creek during July-September of 2011 revealed no temporal shift in distribution; juvenile coho salmon were captured at the same elevation and distance from mainstem on all three sampling events (Tables 3 and 4). Although our repeat temporal sampling events are not labor intensive, or of sufficient numbers to draw statistical conclusions, inter-annual variability observed within-stream upper distributional limits were greater than intra-annual movements associated with summer rearing areas. The patterns in distribution we observed were primarily driven by the presence of age-0 fish; approximately 98% of all fish sampled during the study period were below our size threshold cut-offs for age-1+ fish.

3.5.2 Distribution juvenile coho salmon – Age-1+fish

The presence of age-1+ fish within our study areas suggests that headwater stream habitats of the Little Susitna are used for summer rearing. Age-1+ fish represented less than 2% of all fish captured within sampled stream reaches, yet their distribution encompassed 92%, 79%, and 90% of the total stream length sampled within Swiftwater, Mary's, and Nurse's creeks, respectively. A possible explanation for the low relative abundance of fish in the headwater streams may be that slow-water core habitat areas within the mainstem and adjacent lateral channels were not limited. If this were the case,

then we might infer that the age-1+ fish in our study sites were preferentially selecting to rear within these peripheral headwater habitats. Conversely, if mainstem core habitat areas were limited and density-dependent factors drive older age class fish into peripheral summer rearing habitats, then there was high relative potential for headwater streams to support larger populations of juvenile coho salmon and the Little Susitna salmon stock. However, despite the potential for population dynamics to drive distribution of juvenile coho salmon within the greater Little Susitna watershed, in our study streams, we found insufficient evidence that the distribution of age-1+ fish was driven by habitat configurations.

The upstream distribution limits of age-1+ fish were consistent with distribution limits of all-aged fish. In these upstream areas, percent slope within the stream network increased with increasing elevation (as seen in Bescheta and Platts 1986; Montgomery and Buffington 1997). Without adequate habitat configurations (e.g., pools) favorable for resting and recovery within upper reaches, water velocities that exceed burst and sustained swimming speeds of age-1+ juvenile coho salmon may form barriers to movement. The conditions within the upper reaches may act as a filter preventing further upstream migrations by age-1+ juvenile coho salmon (Poff 1997); they also provide suitable habitat for other sympatric species (e.g., Dolly Varden *Salvelinus malma*) with greater swimming ability. The presence of predators, most notably Dolly Varden, in upper reaches of our study area may also be a driving factor limiting the upstream distribution of juvenile coho salmon. Dolly Varden are known to prey upon juvenile

coho salmon (Dollof and Reeves 1990). In Swiftwater and Mary's creeks, a two-fold increase in Dolly Varden relative abundance was observed in the reach directly upstream of the upper distribution limits of juvenile coho salmon (K. Foley, University of Alaska Fairbanks, personal observation).

3.5.3 Environmental conditions affecting juvenile coho salmon abundance

Our model relating standardized validated estimates of juvenile coho salmon abundance to measured habitat features revealed biologically meaningful relationships for all-aged individuals. Using model parameter estimates (Eq. 2) and holding weighted averaged dominant substrate within the model constant at the mean, we generated model predictions of juvenile coho salmon abundance for our minimum elevation observed at 111m as 430 salmon. For our maximum elevation observed at 383 m, our predicted abundance was 35 individuals within a 100 m section of stream reach. This is an absolute difference of 396 individuals over a 272 m range of elevation. Given that our standardized mean number of individuals predicted in a site was 299, this is a sizeable difference in abundance. For managers seeking to prioritize culvert replacement within the range of elevations in our model, they can anticipate, according to our results, a decrease in abundance of 17 fish per 100 m of stream for every 10 m increase in elevation. However, in addition to elevation, dominant substrate also figured in our model as a predictor for all-aged juvenile coho salmon abundance.

Using model parameter estimates (Eq. 2) and holding the elevation value within the model constant at the mean (Table 1), model predictions of juvenile coho salmon abundance for our minimum value for dominant substrate observed at 4, is 436 salmon. For the maximum value for dominant substrate, our predicted abundance was 135 individuals observed within a 100 m section of stream reach. This is an absolute difference of 300 individuals spanning five substrate types (i.e., sand, small and large gravel, cobble, and boulder). Given that the mean standardized validated number of individuals predicted in a site was 299, this is a sizeable difference in abundance; however, the effects of elevation upon calibrated abundance estimates of juvenile coho salmon dwarfed the effects observed of weighted averaged dominant substrate. This would suggest that within the range of conditions represented by this study, elevation has a greater effect upon calibrated abundance estimates for all-aged individuals than our measure of dominant substrate. Despite our modeling exercise, no clear or biological meaningful relationship emerged between age-1+ individuals, who were more sporadically distributed throughout the system and at generally low numbers. This indicates that occupied stream length is likely the most useful measure for prioritizing these systems for culvert replacement and detailed habitat assessments are likely not a cost-effective approach for understanding the relative value of headwater streams for juvenile coho salmon within the range of conditions represented by this study.

However, our continuous sampling technique allowed us to observe one stream reach within Nurse's Creek that contained an extraordinarily high number of individuals

(n = 69; age-1+ juvenile coho salmon, average abundance in other reaches, n = 15). This reach was the site of a channel connection, which has been associated with high abundance of fish in other systems (Gresswell et al. 2006). Channel connections tend to coincide with high habitat complexity, an influx of drifting insects and allochthonous material, and deep pools (Vannote et al. 1980; Baxter et al. 2004; Benda et al. 2004; Wipfli and Baxter 2010) that may be favorable for age-1+ individuals using headwater streams for rearing. Although we are limited in making any firm conclusions by our single observation, this finding and past research suggest that network complexity in our headwater stream systems could provide more favorable habitat for older juveniles. Therefore, network complexity and the presence of perennial channel connections should be considered for prioritizing stream restoration activities, particularly if no other factors, such as stream length or natural barriers, are useful for differentiating and therefore prioritizing streams slated for restoration. We note that, without a continuous approach to sampling, we could have easily missed this observation.

Habitat configurations within our study sites are spatially autocorrelated up to an approximate distance of 467 m. That is, within our streams, observations within this distance are more spatially similar to another than those further apart (versus 365 m for all-aged fish). If we compare within-stream differences between the upper extents of age-class distributions with our measures of spatial autocorrelation, we find relatively little difference (less than 150 m). Assuming we are able to capture the upper limits of distribution in this manner and based upon evidence from this work, we could also use

network complexity to identify potential abundance hotspots that require sampling. Elevation and percent slope were relatively consistent for describing the upstream distribution limits, suggesting that these factors are more important than distance from the mainstem river. When estimating the amount of stream potentially occupied by fish for prioritizing stream restoration, we suggest the use of elevation to set upstream limits in the absence of information. We encourage further investigation into the role of tributary junctions and network complexity in improving the overall value and productivity of these peripheral areas. These streams do provide spawning habitat for adult coho salmon outside of the mainstem river, and all-aged individuals may use headwater streams for both rearing and passage to downstream habitats. Monitoring temporal changes of distributions within these headwater streams over the long-term is one area we suggest improvements for informing continuing and ongoing restoration activities occurring in the region.

Although the headwater streams represented in our study are unlikely to produce high numbers of coho salmon, it does not follow that peripheral, relatively low productivity habitats like these should be ignored in ongoing restoration efforts in the region. These areas likely represent both complementary and supplementary habitats that increase variability in both life-history and juvenile traits (e.g., fish length and outmigration timing) in the system. This type of variability represents the adaptive potential of the population and could provide spatial complexity in juvenile ecology, or biocomplexity, which, in other systems, improves overall population stability and

resilience to environmental change (Michener et al. 2001; Hillborn et al. 2003). Given the dual threats of climate change and ongoing human development in the area, including both urban and suburban development and proposed hydro projects, this type of variability is likely to be increasingly important for the persistence and continued productivity of this valuable population of Pacific salmon.

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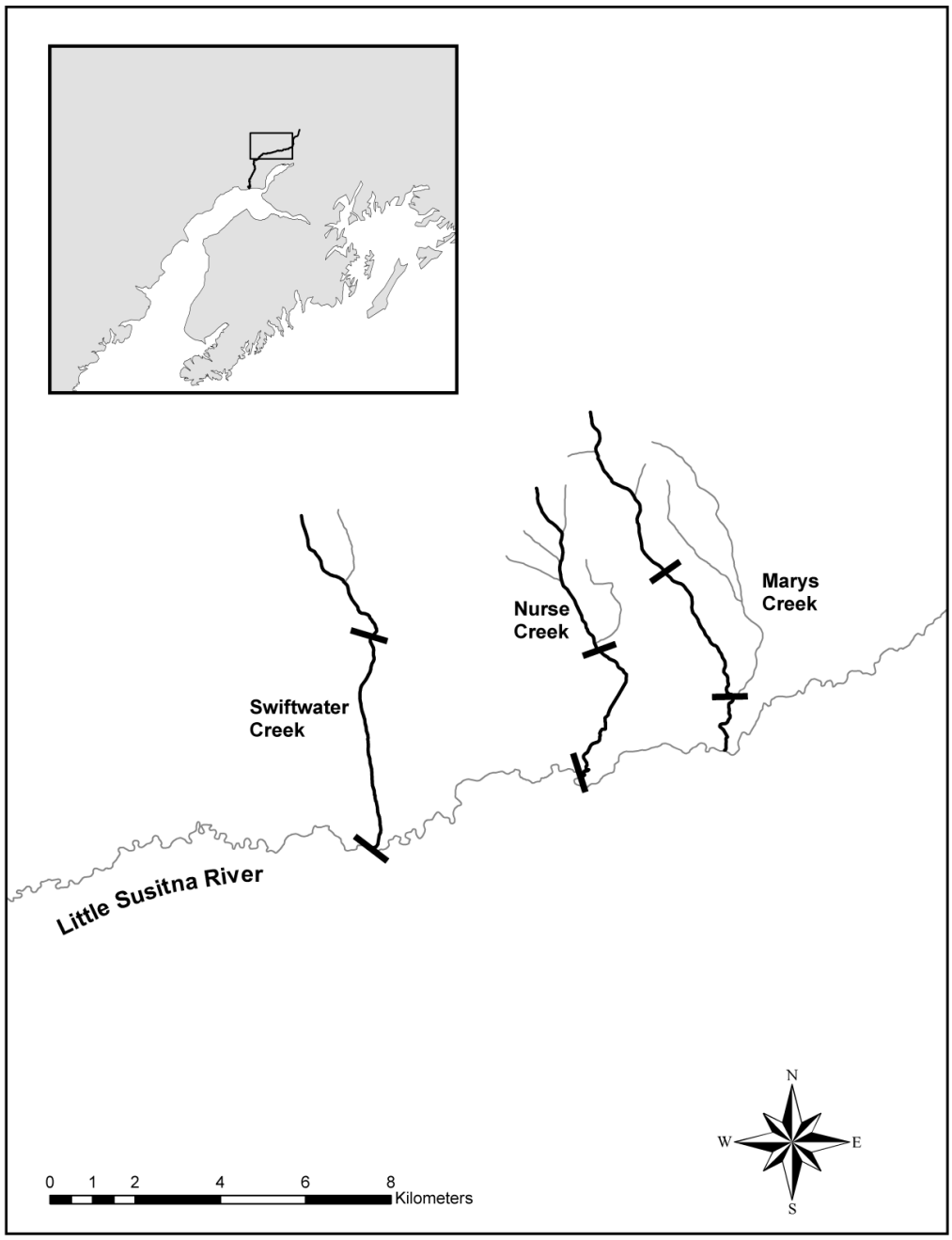


Figure 3.1 Study area map. Headwater streams of the Little Susitna River, Alaska, selected for distribution and abundance sampling. Line markers on the streams indicate the upper and lower boundaries of the study areas.

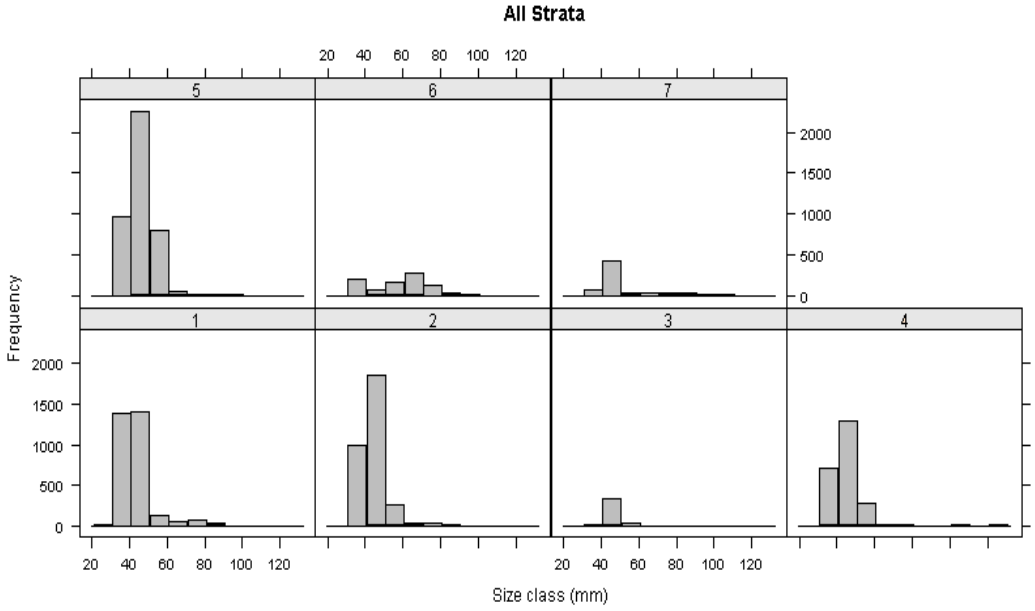


Figure 3.2 Juvenile coho salmon fork-length histograms by strata. Numbered strata are ordered sequentially beginning in the bottom left panel and proceeding to the upper right. Strata 1: Jul 6 – Jul 16, 2010; strata 2: Jul 7 – Jul 29, 2010; strata 3: Aug 3 – Aug 10, 2010; strata 4: Aug 20 – Aug 25, 2010; strata 5: Sept 1 – 15, 2011; strata 6: Jul 5 – Jul 8, 2011; strata 7: Jul 19 – Jul 29, 2011.

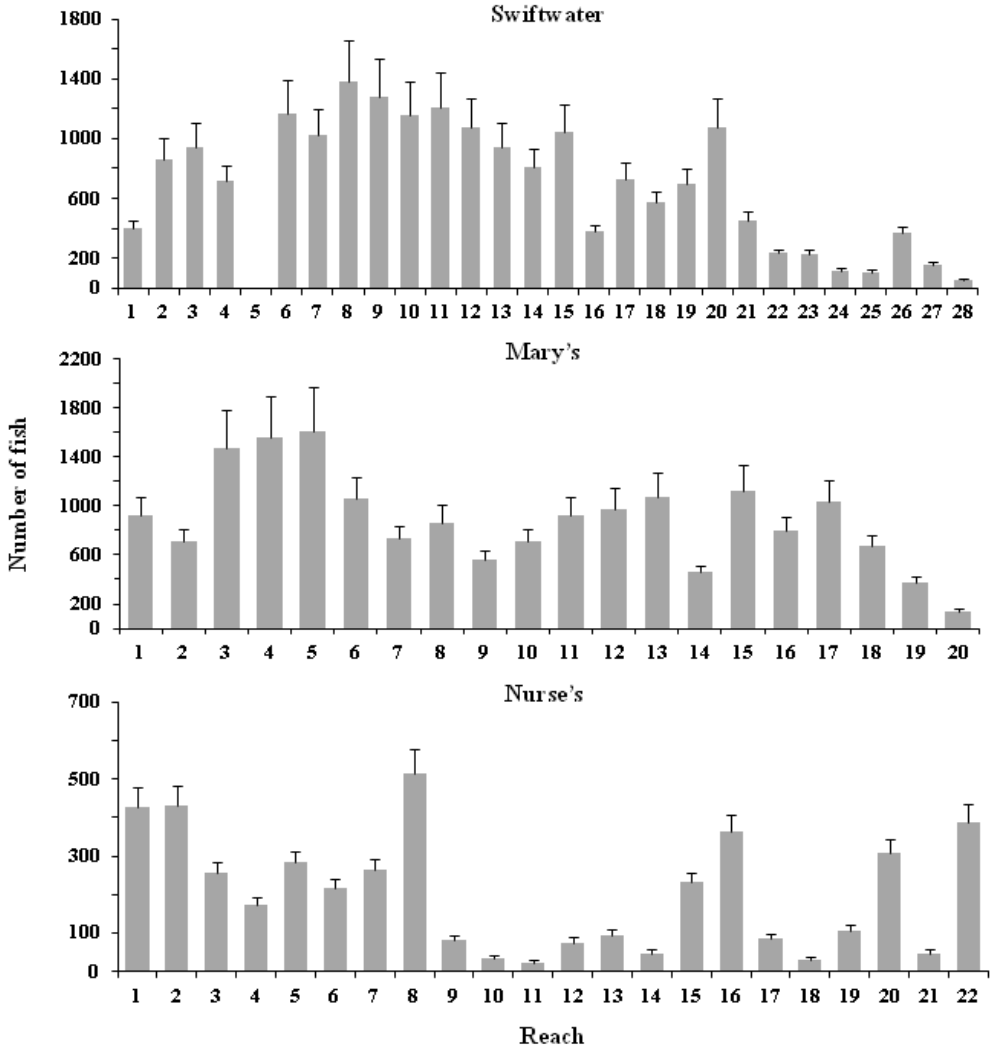


Figure 3.3 All-aged juvenile coho salmon calibrated abundance estimates. Calibrated abundance estimates and upper 95 % confidence intervals for all-aged juvenile coho salmon by stream and reach. All-aged fish are located continuously within each stream reach throughout their distribution for all study streams. In Swiftwater reach five estimates were removed from analyses due to sampling error.

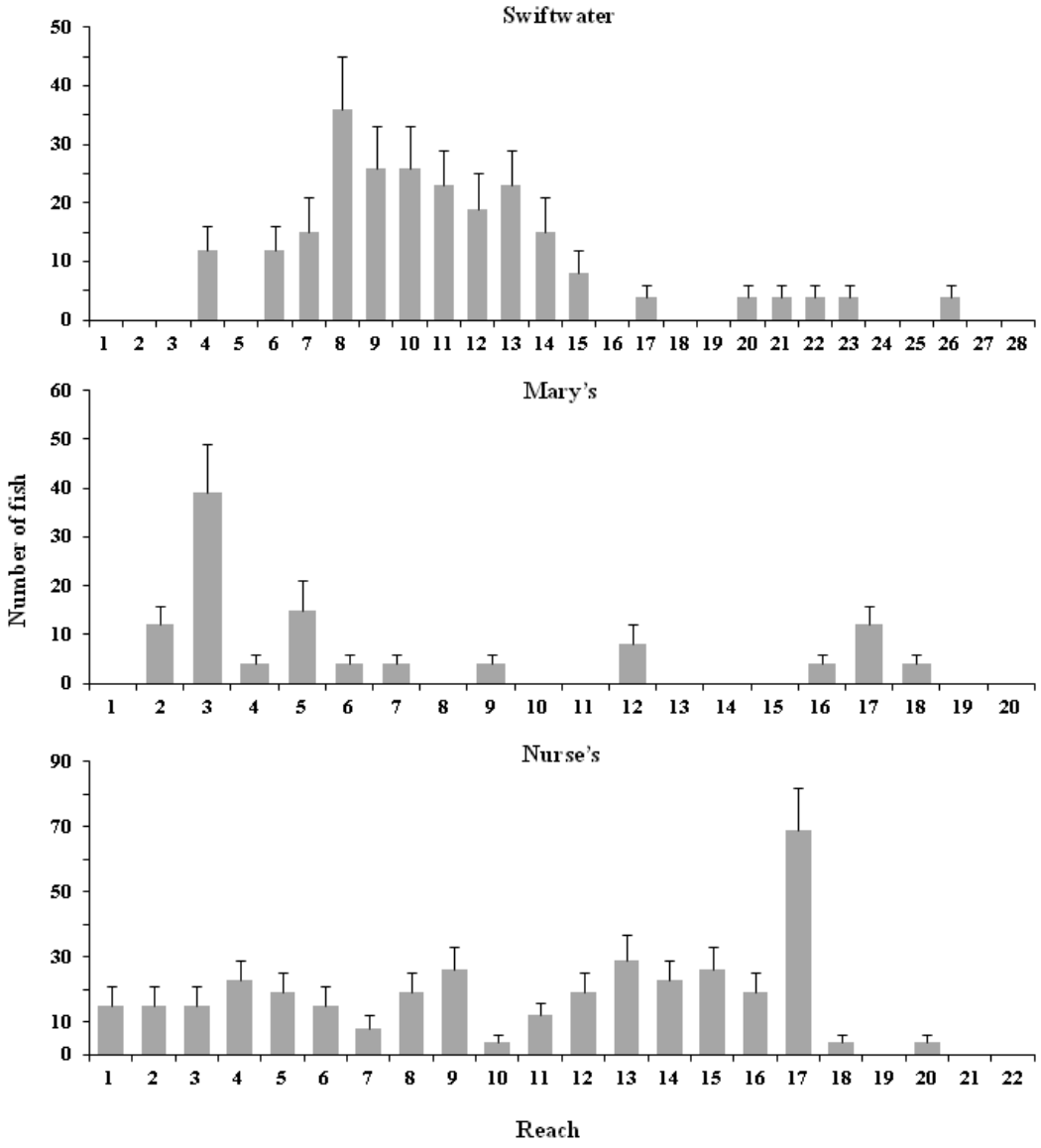


Figure 3.4 Age-1+ juvenile coho salmon calibrated abundance estimates. Calibrated abundance estimates and upper 95% confidence interval for age-1+ juvenile coho salmon by stream and reach. Age-1+ fish are not located continuously within each stream reach throughout their distribution for all study streams. In Swiftwater reach five estimates were removed from analyses due to sampling error.

Table 3.1 Characteristics of study site stream reaches. Characteristics of stream reaches (*n*=69) in headwater streams of the Little Susitna River sampled to estimate juvenile coho salmon abundance and distributions in 2010-2011. Wood classes A-F represent size classes: 1 - 5 m in length; (A) 10 - 50 cm dia.; (B) greater than 50 cm dia., and greater than 5 m in length (C) 10 - 50 cm dia.; (D) greater than 50 cm dia., Rootwads; (E), and Snags (clusters of wood pieces not of size class A-E; (F).

Variable	Abbreviation	Mean	SD	Range
Slope (%)	PS	2.8	1.6	0–7.5
Max Daily Avg Temp (°C)	MDAT	9.9	0.6	9.0–11.3
Elevation (m)	EV	192.9	41.2	110.9–383.3
Mean cross section (m^2)	CS	0.9	0.4	0.3–1.9
Stream reach length (m)		205.0	25.5	104.1–300.2
Channel connections	CC	0.2	0.5	0–2
Weighted average dominant substrate	DS	6	1	4–8
Total undercut bank (m)	UB	47.5	29.9	8.3–123
Wood AB (#/ m)*	WAB	0.6	0.3	0.1–1.6
Wood CD (#/m)*	WCD	0.1	0.0	0.0–0.2
Wood E (#/m)*	WE	0.0	0.0	0.0–0.04
Wood F (#/m)*	WF	0.0	0.0	0.0–0.1

* indicates a variable standardized to stream reach length

Table 3.1 (continued)

Variable	Abbreviation	Mean	SD	Range
Total pool area (m^2)	PA	242.0	133.4	14.5–652
Mean fish size (mm)	MnFS	50.7	10.3	40–84
Standardized abundance estimates (all-aged)		299	224	10–838
Standardized abundance estimates (age-1+)		5	6	0.0–33

* indicates a variable standardized to stream reach length

Table 3.2 Age as predicted by scale samples by three independent observers. Comparison of age as predicted by scale samples (*N*=83) and fork length size classes (mm) by three independent observers.

Size class	Observer 1		Observer 2		Observer 3		*N*
	Age -0	Age-1	Age-0	Age-1	Age-0	Age-1	
41–50	4		4		4		4
51–60	8		8		8		8
61–70	18	1	19		19		19
71–80	10	8	11	7	10	8	18
81–90	1	18	1	18	1	18	19
91–100		9		9		9	9
101–110		4		4		4	4
111–120		1		1		1	1
>121		1		1		1	1

Table 3.3 Average elevation at upstream distribution limit. Average elevations (m) at upstream distribution limit for distribution of juvenile coho salmon sampled within three headwater streams, Alaska 2010 and 2011. Numbers in parenthesis represent numerical stream reach designations.

	Swiftwater		Mary's		Nurse's	
	All-aged	Age-1+	All-aged	Age-1+	All-aged	Age-1+
2010						
July						
Aug	289 (28)	267 (26)				
Sept	289 (28)		265 (20)	238 (17)		
2011						
July	267 (26)		283 (22)		240 (22)	230 (20)
Aug	267 (26)		283 (22)		240 (22)	
Sept	267 (26)		283 (22)		240 (22)	
Mean elevation (m)	278	267	275	238	240	230

Table 3.4 Landscape scale variables describing the upper extent of distribution. Stream reach numerical designation and associated landscape scale variables describing the upper extent of coho distribution within three headwater streams, Alaska sampled in 2010 and 2011.

Reach	Elevation (m)	Distance to mainstem (m)	Slope (%)
Swiftwater			
26	267	5,015	4
28	289	5,408	5
Mary's			
17	238	4,181	6
20	265	4,845	5
22	283	5,290	5
Nurse's			
20	230	4,002	3
22	240	4,422	5

Table 3.5 Candidate models examined for the best approximating model. Candidate models examined for determining the best approximating linear mixed-effects models (acc *wi*, ≤ 0.95) examining the effect of landscape and local scale variables on calibrated abundance estimates of all-aged juvenile coho salmon in headwater streams in Alaska. Variables include elevation (EV), weighted average dominant substrate (DS), pool area (PA), wood size class E (WE), and wood size class CD (WCD).

	Candidate model	*k*	logLik	AIC corr	Δ_i	w_i	acc *wi*	ER
1	EV + DS	6	-193.57	399.14	0	0.76	0.758	
2	EV	5	-196.81	403.62	4.48	0.08	0.839	1
3	EV + DS + PA + WE + WCD	9	-193.16	404.33	5.19	0.057	0.895	9.4
4	EV + PA	6	-196.58	405.17	6.03	0.037	0.933	13.4
5	EV + WE	6	-196.6	405.2	6.06	0.037	0.969	20.4
6	WE + WCD + DS + PA	8	-194.92	405.84	6.70	0.027	0.996	20.7
7	We + WCD + PA	7	-198.21	410.43	11.29	0.0027	0.999	28.5
8	Null model- intercept only	4	-201.8	411.59	12.45	0.0015	1	282.6

Table 3.6 Effect size for models of all-aged juvenile coho salmon abundances. The absolute effect size (number of fish captured per 100 m) for models of all-aged juvenile coho salmon abundance anticipated over the range of conditions found within (n=69) stream reaches of headwater streams, Alaska, sampled in 2010 and 2011. Parameters in the predictive model include elevation (EV) and weighted average dominant substrate (DS).

Variable	Mean	Minimum	Maximum	Absolute effect size
EV	192.9	110.8	383.3	396
DS	6	4	8	300

Table 3.7 Models examined for inclusion into the best model confidence set. All models examined for inclusion into the 95% confidence set of best-ranked linear models (acc w_i, ≤ 0.95) examining the effect of landscape and local scale variables on calibrated abundance estimates of age-1+ juvenile coho salmon in headwater streams in Alaska. Variables within candidate models are elevation (EV), percent slope (PS), wood size class CD (WCD), weighted average dominant substrate (DS), and mean cross-section (CS).

	Candidate model	k	logLik	AIC corr	Δ_i	w_i	acc w_i	ER
1	EV + PS	5	-82.26	175.47	0	0.40	0.39	
2	WCD + DS	5	-82.59	176.14	0.68	0.29	0.66	1
3	Null model- intercept only	3	-84.97	176.30	1.42	0.16	0.85	1.40
4	WCD + DS + EV + PS + CS	8	-80.85	180.11	3.19	0.09	0.93	2.04
5	CS*	4	-84.96	178.54	3.40	0.07	1	4.93

*Indicates acc w_i. ≥ 0.95.

Table 3.8 Model-averaged estimates included within the best predictive model. Model-averaged estimates under consideration (±SE), ranked in order of relative importance, and interpreted as equivalent to the probability that the predictor is a component of the best model. LCL and UCL are lower and upper 95% confidence limits on parameter estimates, respectively. Estimates are for five environmental variables predicting abundance of juvenile coho salmon. Variables include elevation (EV), percent slope (PS), wood size class CD (WCD), weighted average dominant substrate (DS), and mean cross-section (CS).

Variable	Predictor weight	Model averaged parameter estimate (±SE)	LCL	UCL
Intercept	1	2.68 (0.769)	1.17	4.18
EV	0.50	-0.005 (<0.001)	-0.013	0.002
PS	0.50	0.007 (<0.001)	-0.004	0.018
WCD	0.38	0.912 (3.96)	-1.04	2.86
DS	0.38	-0.085 (0.085)	-0.25	0.081
CS	0.08	0.023 (0.079)	-0.131	0.177

Appendix3.A

Age comparison as predicted by juvenile coho scale samples. Comparison of age as predicted by scale samples (N = 83) and fork length (mm) by three independent observers. Values of 0 and 1 represent age-0 and age-1+ respectively.

Fork length	Observer 1 age	Observer 2 age	Observer 3 age
44	0	0	0
44	0	0	0
46	0	0	0
49	0	0	0
51	0	0	0
51	0	0	0
53	0	0	0
55	0	0	0
55	0	0	0
57	0	0	0
59	0	0	0
60	0	0	0
61	0	0	0
61	0	0	0
61	0	0	0

Appendix 3.A (continued)

Fork length	Observer 1 age	Observer 2 age	Observer 3 age
61	0	0	0
61	0	0	0
61	0	0	0
62	0	0	0
62	0	0	0
63	0	0	0
63	0	0	0
63	0	0	0
63	0	0	0
63	0	0	0
63	0	0	0
64	0	0	0
67	0	0	0
67	0	0	0
68	1	0	0
68	0	0	0
72	0	0	0
73	0	0	0

Appendix 3.A (continued)

Fork length	Observer 1 age	Observer 2 age	Observer 3 age
74	0	0	0
74	0	0	0
75	0	0	0
76	1	1	1
76	0	0	0
78	1	1	1
78	1	1	1
78	1	1	1
78	0	1	0
78	0	0	1
78	0	0	0
79	1	1	0
79	1	0	1
79	1	1	1
80	0	0	0
80	1	0	1
81	0	0	0
81	1	1	1

Appendix 3.A (continued)

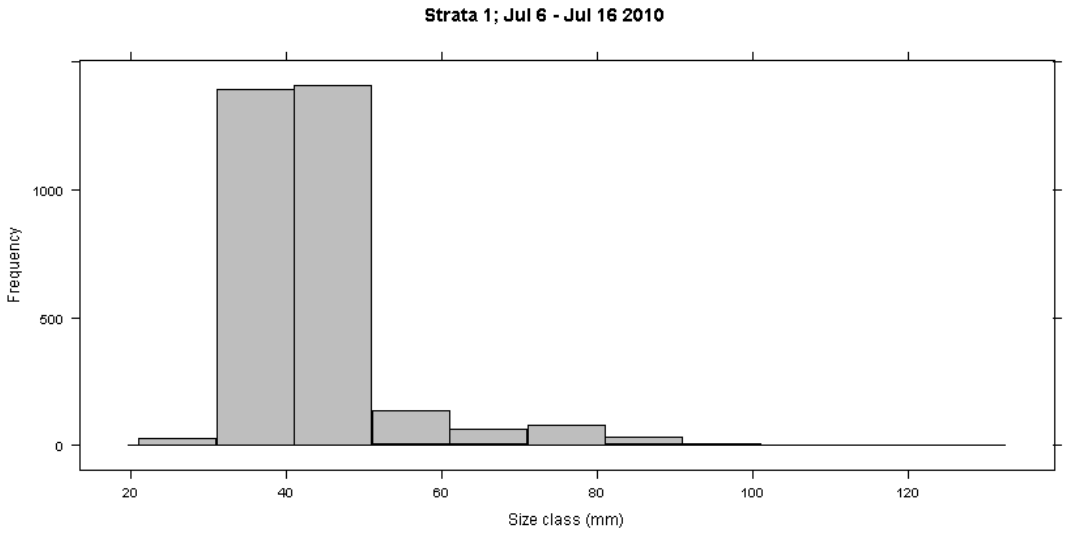
Fork length	Observer 1 age	Observer 2 age	Observer 3 age
82	1	1	1
82	1	1	1
82	1	1	1
82	1	1	1
82	1	1	1
84	1	1	1
84	1	1	1
85	1	1	1
85	1	1	1
86	1	1	1
86	1	1	1
86	1	1	1
86	1	1	1
87	1	1	1
87	1	1	1
88	1	1	1
88	1	1	1
91	1	1	1

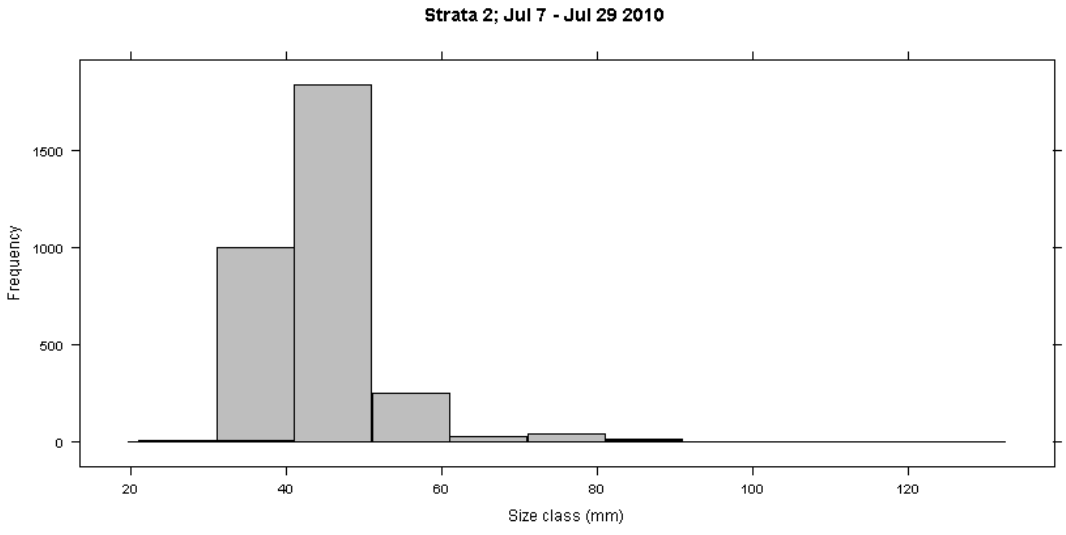
Appendix 3.A (continued)

Fork length	Observer 1	Observer 2	Observer 3
	age	age	age
92	1	1	1
92	1	1	1
94	1	1	1
94	1	1	1
94	1	1	1
97	1	1	1
97	1	1	1
98	1	1	1
100	1	1	1
102	1	1	1
104	2	2	2
105	2	2	2
108	2	2	2
116	2	2	2
129	2	2	2

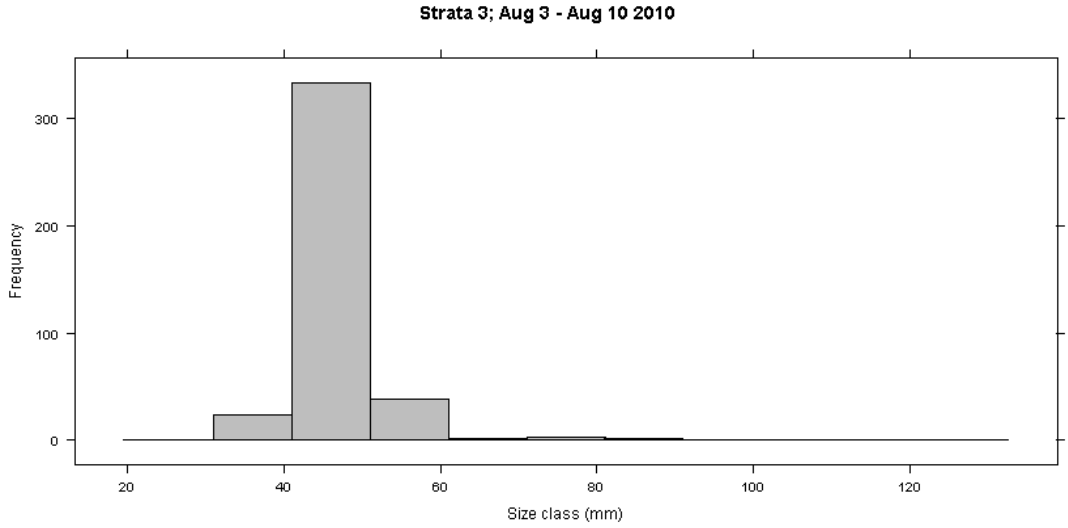
Appendix 3.B

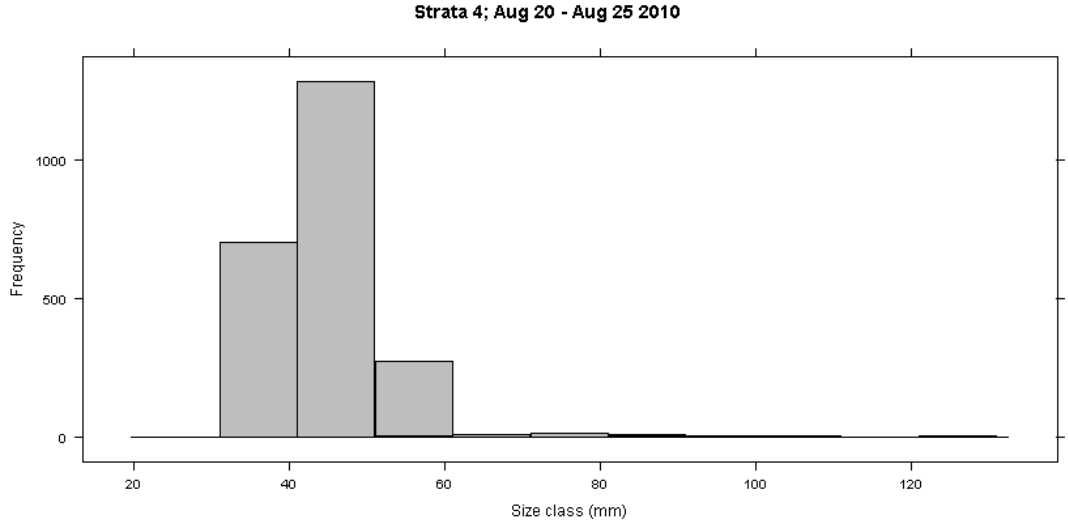
Histograms of fish fork length by strata for juvenile coho salmon. Histograms of fish fork length by strata for juvenile coho salmon captured in headwater streams in 2010 and 2011. Note difference in y-axis values among histograms. Information presented here contains duplicate information presented in Table 2 but with more detail to clarify size thresholds.





Appendix 3.B (continued)





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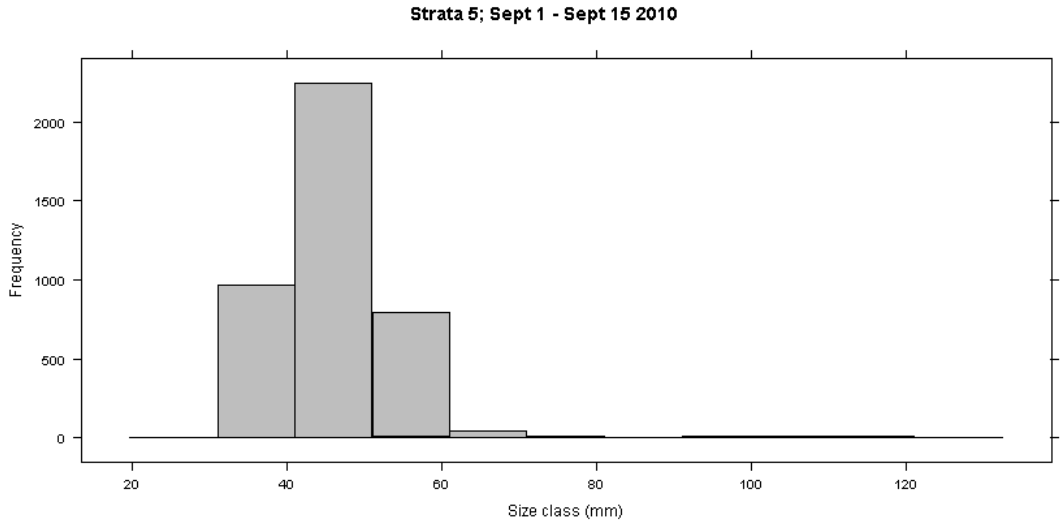

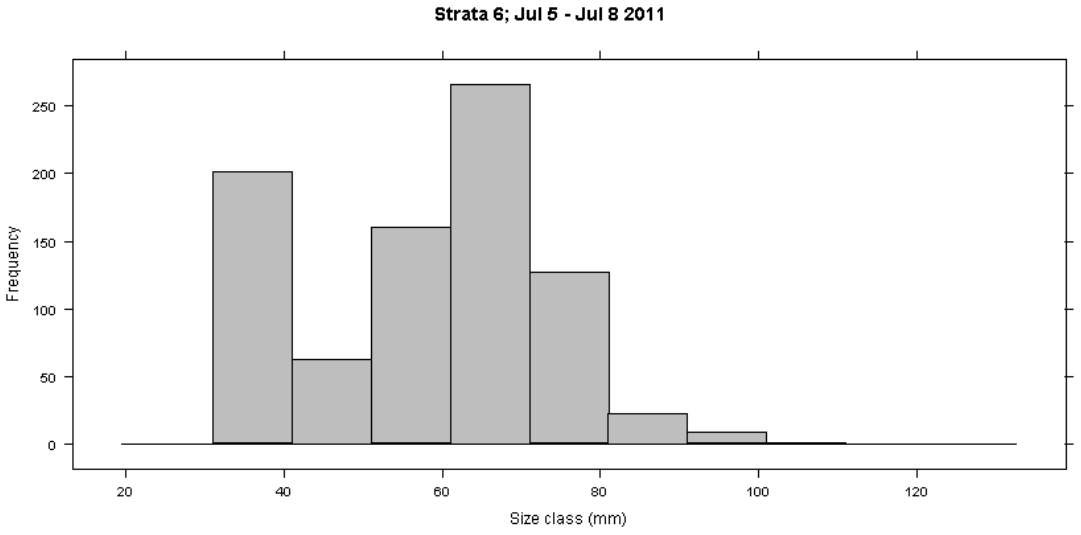

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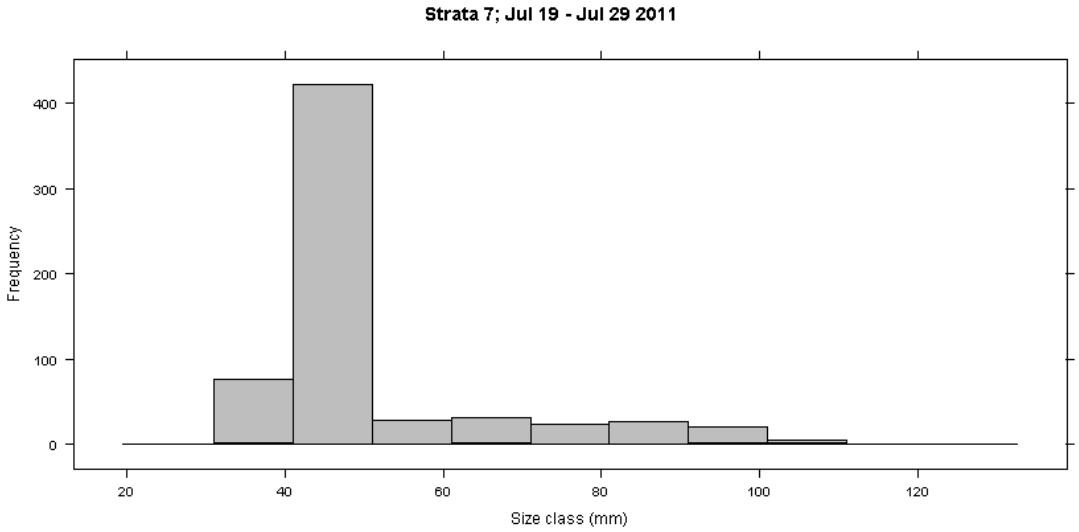

Appendix 3.C

Spearman's correlation matrix of age-1+ predictor variables. Spearman's correlation matrix of all variables under consideration as independent variables predicting calibrated relative abundance estimates of age-1+ juvenile coho salmon occurring within headwater streams, Alaska, 2010 and 2011.

	DM	PS	MDAT	EV	CS	CC	DS	UB	WAB	WCD	WE	WF	PA
DM	1.00												
PS	0.61	1.00											
MDAT	-0.97	-0.53	1.00										
EV	0.97	0.53	-1.00	1.00									
CS	0.12	0.21	-0.06	0.07	1.00								
CC	0.16	0.33	-0.11	0.11	0.13	1.00							
DS	0.52	0.42	-0.41	0.41	0.58	0.25	1.00						
UB	-0.38	-0.51	0.28	-0.28	-0.45	-0.34	-0.67	1.00					
WAB	-0.43	-0.44	0.30	-0.30	-0.11	-0.26	-0.65	0.56	1.00				
WCD	-0.04	0.12	0.09	-0.09	0.23	0.20	-0.04	-0.06	0.09	1.00			
WE	0.42	0.26	-0.33	0.33	0.10	0.14	0.37	-0.23	-0.43	0.09	1.00		
WF	-0.09	-0.18	0.00	-0.01	-0.49	-0.15	-0.61	0.49	0.43	0.03	-0.03	1.00	
PA	-0.34	-0.41	0.28	-0.28	0.20	-0.11	-0.20	0.38	0.36	0.30	-0.03	0.16	1.00

Distance to main stem (DM), percent slope (PS), maximum daily averaged temperature (MDAT), elevation (EV), averaged cross-section (CS), channel connections (CC), weighted average dominant substrate (DS), total length of undercut bank (UB), wood pieces size classes A and B per m (WAB), wood pieces size classes C & D per m (WCD), wood pieces size class E per m WE), wood pieces size class F per m (WF), total pool area (PA).

Appendix 3.D: Stream temperature model by elevation

A.3.D.1 Introduction

Temperature is one of the most important environmental factors controlling the distribution and behavior of fishes (Magnuson et al. 1979). Fish often inhabit a specific thermal niche where they optimize physiological performance, though temperature preference may be balanced against other physiological or ecological filters (e.g. Brett 1971; Coutant and Carroll 1980; Poff 1997). Although temperature requirements and preferences vary with life stage, the interest and relevance to this study are thermal preferences and tolerances exhibited during the juvenile life stages and freshwater occupancy.

A vast amount of the literature quantifying the relationship between temperature and developmental rates of salmonids aims to improve production in hatcheries Therefore, the positive non-linear relationship between temperature and the rate of development of embryos and alevins is well documented (e.g., Velsen 1987; Murray and McPhail 1988; Beacham and Murray 1990; Murray et al. 1990;). Studies indicate that time to hatching and emergence would advance substantially with increasing surface water temperatures. Coho salmon embryo and alevin development and survival rates were optimized at 4 or 5 ^{0}C, and mortality generally occurred at 14 or 15 ^{0}C (Murray et al. 1990). Further study of embryo survival in laboratory experiments witnessed an

increase in mortality at 11 ^{0}C, with an upper limit for embryonic development at 14 ^{0}C (Murray and McPhail 1988).

With regard to thermal preferences, Brett (1952) reported a 'preferendum' (temperature most frequently selected) for juvenile coho salmon of 11–12 ^{0}C. He also determined that juvenile coho salmon generally avoided stream temperatures above 15 ^{0}C, but that they showed the greatest preference for temperatures between 12–14 ^{0}C. Bell (1986) noted that preferred water temperatures for juvenile coho juvenile salmon ranged from 11.7–14.5 ^{0}C. Konecki et al. (1995) found that temperature preference of juvenile coho salmon was 10–12 ^{0}C and that fish exhibited a great deal of variation with their thermal preference suggesting that, although some genetic based variation in thermal preference exists, the species is highly tolerant of larger temperature fluctuations. The upper thermal tolerance of juvenile coho salmon is 25.0 ^{0}C (Bell 1986). Thomas et al. (1986) performed studies investigating the mortality of coho salmon subjected to high fluctuations in temperature. They concluded for fish acclimated to a 10–13 ^{0}C cycle was 28 ^{0}C for age-0 fish, slightly higher than previous investigations indicated.

To understand how thermal conditions may influence populations of coho salmon juveniles in our study sites within headwater streams of the Little Susitna drainage, I compiled data from temperature loggers placed at intervals in the stream. Maximum daily average temperature (MDAT) covaried with elevation and was removed from consideration as a predictor variable for exploring relationships between environmental

variables and distribution of juvenile coho salmon cohorts. However, despite the strong covariance between the two (Appendix 3.3), and our inclusion of elevation as a covariate within the averaged model for all-aged fish (Chapter 3; Table 5), we feel it is important to note that fish may be responding to stream temperature. As such, we feel this thermal data warrants some attention.

A.3.D.2 Methods

Stream water temperature was monitored throughout the study period to develop thermal profiles of our study area and to explore relationships between elevation and stream water temperature. Thirty-five Hobo Tidbit v2 temperature loggers were deployed throughout all study streams. Temperature logger deployment within Swiftwater and Mary's creeks occurred in 2010, and in 2011, temperature loggers were deployed within Nurse's Creek immediately after break-up. Stream temperatures used in the model development included only measurements recorded in 2011 from within Swiftwater and Mary's creeks. For a detailed description of field and analytical methods pertaining to our stream temperature data loggers and methods for calculating our metric of stream temperature, maximum daily averaged temperature (MDAT), please review the methods section of chapter three.

A.3.D.3 Results and Discussion

The total stream temperature loggers deployed were $n = 14$, $n = 10$, and $n = 11$, within Swiftwater, Mary's, and Nurse's creeks, respectively. Maximum daily average temperature can be predicted as:

$$\mathrm{MDAT} \sim 1.34\mathrm{E}^{+01} - 2.56\mathrm{E}^{-02}(\mathrm{EV}) + 3.58\mathrm{E}^{-05}(\mathrm{EV}^2) \qquad \text{(Eq. 1)}$$

Where both a linear and quadratic term for elevation (EV) are the only predictor variables in the equation ($R^2 = 0.8289$).

Although 2011 was the only year we had stream temperature data for all three streams, we removed Nurse's Creek from model development, justified by the lack of elevation data across all of our study streams at higher elevations; no stream temperature data corresponding to higher elevations were available for Nurse's Creek. The discovery of an undocumented culvert pipe within the stream precluded further sampling above the structure.

Incorporating a stream effect into our model proved to be a more statistically significant predictor of MDAT (R^2=0.95) than without ($R^2 = 0.8289$). However, although incorporating a stream effect may be statistically significant, and we recognize it in our model development, we have no way to isolate the specific effect and therefore opt for the more parsimonious model (Eq. 1). Using our model, we predicted MDAT for known

elevations within Nurse's Creek and compared these to actual MDAT measurements. Only two actual measurements did not lie within 95% CI for predicted values of MDAT (Table 1). Should temperature preferences be the limiting factor for upstream distribution of either juvenile salmon or spawning adult females in the Little Susitna drainage, this model may prove useful for estimating upstream limits to their distribution via estimation of thermal conditions within these headwater streams. We note that regional differences in elevation/thermal gradients and the effects of such factors as groundwater influx, etc. are not incorporated into the model; therefore its transferability outside of the Little Susitna drainage is limited.

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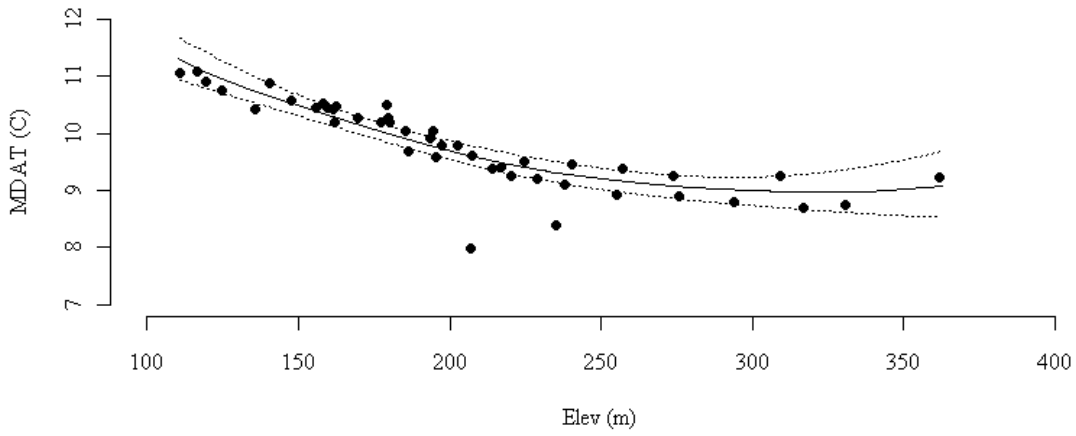

Figure A.3.D.1 Predicted values of stream temperature and elevation. Relationship between predicted values of maximum daily average temperature (MDAT) and elevation as determined within two headwater streams of the Little Susitna River, Alaska in 2011. Dashed lines represent 95% confidence intervals.

Table A.3.D.1 Maximum daily averaged stream temperature summaries. Stream temperature summaries for maximum daily average temperature, (MDAT) values for observed (MDAT actual), and predicted (MDAT fit), values. MDAT fit values are based upon elevation. Upper and lower 95% confidence levels are shown for all predicted values (95 LCL & 95 UCL), respectively.

Logger no.	Stream	EV (m)	MDAT actual (^{0}C)	MDAT fit (^{0}C)	95 LCL	95 UCL
1	Swiftwater	110.86	11.06	11.30	10.37	12.23
2	Swiftwater	115.31	11.08	11.20	10.28	12.12
3	Swiftwater	117.93	10.90	11.14	10.23	12.05
4	Swiftwater	120.70		11.08	10.17	11.99
5	Swiftwater	124.87	10.76	10.99	10.09	11.89
6	Swiftwater	129.22		10.90	10.01	11.79
7	Swiftwater	135.51	10.43	10.77	9.88	11.65
8	Swiftwater	140.72		10.66	9.79	11.54
9	Swiftwater	147.82	10.57	10.53	9.66	11.40
10	Swiftwater	150.42		10.48	9.61	11.35
11	Swiftwater	157.60	10.46	10.35	9.48	11.22
12	Swiftwater	158.15		10.34	9.47	11.21
13	Swiftwater	161.66	10.43	10.28	9.41	11.15
14	Swiftwater	168.61		10.16	9.30	11.03
15	Swiftwater	178.30	10.49	10.01	9.14	10.87
16	Swiftwater	189.53		9.85	8.98	10.71

Table A.3.D.1 (Continued)

Logger no.	Stream	EV (m)	MDAT actual (^{0}C)	MDAT fit (^{0}C)	95 LCL	95 UCL
17	Swiftwater	194.66	10.05	9.77	8.91	10.64
18	Swiftwater	202.09		9.68	8.81	10.55
19	Swiftwater	208.96	9.85	9.59	8.73	10.46
20	Swiftwater	216.34		9.51	8.64	10.38
21	Swiftwater	222.51	9.71	9.44	8.57	10.31
22	Swiftwater	230.75		9.36	8.49	10.23
23	Swiftwater	240.53	9.72	9.28	8.40	10.15
24	Swiftwater	249.25		9.21	8.34	10.08
25	Swiftwater	257.31	9.66	9.15	8.28	10.03
26	Swiftwater	266.60		9.10	8.23	9.97
27	Swiftwater	274.57		9.06	8.18	9.94
28	Swiftwater	289.33		9.01	8.13	9.89
29	Mary’s	177.24	10.69	10.03	9.16	10.89
30	Mary’s	177.25		10.03	9.16	10.89
31	Mary’s	179.63	10.27	9.99	9.12	10.85
32	Mary’s	182.20		9.95	9.09	10.82
33	Mary’s	185.56	10.17	9.90	9.04	10.77
34	Mary’s	188.57		9.86	8.99	10.72
35	Mary’s	193.53	9.93	9.79	8.92	10.66

Table A.3.D.1 (Continued)

Logger no.	Stream	EV (m)	MDAT actual (^{0}C)	MDAT fit (^{0}C)	95 LCL	95 UCL
36	Mary's	196.30		9.75	8.89	10.62
37	Mary's	197.56	9.79	9.74	8.87	10.60
38	Mary's	199.02		9.72	8.85	10.58
39	Mary's	206.13	9.79	9.63	8.76	10.50
40	Mary's	210.22		9.58	8.71	10.45
41	Mary's	214.17	9.39	9.53	8.66	10.40
42	Mary's	217.85		9.49	8.62	10.36
43	Mary's	228.70	9.21	9.38	8.51	10.25
44	Mary's	234.09		9.33	8.46	10.20
45	Mary's	238.17	9.11	9.30	8.42	10.17
46	Mary's	250.87		9.20	8.32	10.07
47	Mary's	255.54	8.93	9.17	8.29	10.04
48	Mary's	265.19		9.11	8.23	9.98
49	Nurse's	141.38	11.06	10.65	9.77	11.53
50	Nurse's	151.19		10.47	9.60	11.34
51	Nurse's	152.57	10.53	10.44	9.57	11.31
52	Nurse's	156.38		10.37	9.50	11.24
53	Nurse's	159.59	10.46	10.32	9.45	11.18
54	Nurse's	161.08		10.29	9.42	11.16
55	Nurse's	165.00	10.20	10.22	9.36	11.09

Table A.3.4.1 (Continued)

Logger no.	Stream	EV (m)	MDAT actual (^{0}C)	MDAT fit (^{0}C)	95 LCL	95 UCL
56	Nurse's	167.32		10.18	9.32	11.05
57	Nurse's	169.74	10.48	10.14	9.28	11.01
58	Nurse's	172.19		10.11	9.24	10.97
59	Nurse's	175.84	10.28	10.05	9.18	10.91
60	Nurse's	182.78		9.94	9.08	10.81
61	Nurse's	186.35	9.69	9.89	9.02	10.76
62	Nurse's	190.35		9.83	8.97	10.70
63	Nurse's	195.66	9.34	9.76	8.89	10.63
64	Nurse's	200.87		9.69	8.83	10.56
65*	Nurse's	208.09	7.99	9.60	8.74	10.47
66	Nurse's	215.02		9.52	8.65	10.39
67	Nurse's	220.49	8.99	9.46	8.59	10.33
68	Nurse's	229.85		9.37	8.50	10.24
69*	Nurse's	235.31	8.39	9.32	8.45	10.19
70	Nurse's	240.03		9.28	8.41	10.15

*Denotes where actual values did not fall within 95% confidence intervals of predicted values.

Chapter 4: Conclusions

The overarching goal of this study was to attain a greater understanding of habitat use characteristics and habitat conditions that affect or limit the distribution of juvenile coho salmon in headwater streams of the Little Susitna River. By using a continuous sampling approach on the landscape, I can provide insight into processes driving distribution and abundance that are critical for the conservation, management and long-term stewardship of the species. Headwater streams often go unrecognized as important habitats for salmon populations. However, they are refugia in the event of a disturbance in the mainstem river, represent an important life history component of the larger population, and may be most reflective of the dynamics of the larger population of coho salmon in the region (Isaak et al. 2003).

To assure that low-effort continuous sampling over large spatial scales provided an accurate representation of abundance and distribution, sources of estimation bias (e.g., habitat-mediated sampling efficiency) and imprecision must be addressed. To determine how biotic and abiotic habitat variables affected low-effort backpack electrofisher sampling efficiency, I validated my sampling methods with closed-population mark-recapture sampling. I found that, within the range of conditions expressed across my study sites, measures of site scale and landscape scale habitat features had no measurable effect upon my sampling efficiency. Specifically, I showed that my single-pass-catch explained 94.8% of the variation expressed in log-transformed mark-recapture estimates,

suggesting single-pass electrofisher sampling may be used as a suitable index of abundance provided sampling methods are validated. These findings are extremely beneficial to resource managers as the lower effort associated with this technique allows an increase in sampling extent to the watershed level (Bateman et al. 2005; Gresswell et al. 2006; Torgersen et al. 2006; Torgersen et al. 2007), with some cost in precision and accuracy of abundance estimates (Rosenberger and Dunham 2005).

The use of headwater streams as nursing and rearing habitat for juvenile coho salmon production is poorly documented; little is known about the relative contribution of these areas to support healthy and viable populations of Little Susitna salmon stocks. To determine the relative use of these habitats by juveniles, I determined and characterized the upstream distributional limits of multiple age cohorts. Young salmon were distributed over the entire stream extent to their upper distributional limits within each of my sampled streams. The mean elevation within Swiftwater Creek occurred at 278 m and 267 m for all-aged and age-1+ fish, respectively, as compared to Mary's Creek, where the mean elevation was 275 m and 238 m for all-aged and age-1+ fish, respectively. Similarities in elevational upstream limits between age classes within and between streams, as well as inter-annual variability, suggests elevation may be used to set the upstream limits of distribution. Short-term temporal changes in the upstream extent of juvenile coho salmon for all study streams through repeat sampling revealed no change in the upper distributional limits for all-aged fish within a growing season and marginal inter-annual changes.

Throughout the occupied stream length, I characterized available habitat and related habitat configuration to validated abundance patterns of juvenile coho salmon by cohort. I determined a fork-length size class threshold of 81 mm, distinguishing between all-aged and age-1+ juvenile coho salmon. This was consistent with findings of Gerken and Sethi (2013), who also reported on lengths of juvenile coho salmon. Patterns of distribution were driven by the presence of all-aged fish, as nearly 98% of all fish sampled over the study period were below my size threshold cut-off value of 81 mm; however, age-1+ individuals were also found throughout the occupied stream length. My models relating validated abundance estimates to habitat variables revealed elevation and weighted average dominant substrate were negatively related to abundance for all-aged fish. However, no clear or biologically meaningful relationships emerged for age-1+ individuals, who were sporadically distributed throughout the system at generally low numbers.

This thesis provided information on juvenile coho salmon distribution and abundances in headwater streams of the Little Susitna River that will allow for strategic and informed management of these populations. For example, the replacement of culverts can be prioritized for those systems heavily used by older, upstream-moving age classes of juvenile salmon as they seek summer rearing habitats. Further, priority can be given to those streams that have the greatest extent of usable stream length and to streams containing tributary junctions and channel connections. Finally, my validation provides

local managers with information on single-pass sampling efficiency of juvenile coho salmon, which will dictate how much effort is required for reliable assessment of juvenile salmon distribution in the area. Further, catch data from similar habitats can be calibrated to reflect juvenile coho salmon abundance, which will dramatically increase information on those populations. Finally, my findings increase our understanding of the fundamental niche of juvenile coho salmon, allowing managers to identify important risks that limit the distribution of this species within this watershed and similar headwater environments.

Given the findings of this work, I offer area managers the following recommendations: 1) Length of occupied stream and elevation limits for juveniles are good indicators of the relative value of headwater streams in the Little Susitna watershed. 2) Network connections and tributary junctions are potentially important for older-age juvenile coho salmon, and prioritization should be given to streams with greater network complexity. 3) Given an autocorrelation of approximately 287 meters, representative reach approaches can consider that spacing when selecting sampling sites.

4.1 References

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